Swain, D. P.[1], A. J, Derksen[2], and J. S. Loch[3]. 1980

A literature review of life histories of some species of fish - rainbow smelt *Osmerus mordax* , gizzard shad *Dorosoma cepedianum* paddlefish *Polyodon spathula*, . shovelnose sturgeon *Scaphirhynchus platorynchus* , pallid sturgeon *Scaphirhynchus albus* and shortnose gar *Lepisosteus platostomus* - that may be introduced into the Hudson Bay watershed from the Missouri River watershed as a result of the Garrison Diversion. Fisheries Branch, Manitoba Department of Natural Resources, MS Report No. 80- 37.

ABSTRACT

A number of fish species now occur in the Missouri River watershed that are not found in the Hudson Bay watershed. Completion of the Garrison Diversion Project in North Dakota as proposed in 1976 will provide a high volume connection between the waters of the two watersheds. Rainbow smelt, gizzard shad, paddlefish, shovelnose and pallid sturgeon and shortnose gar are some of the species that may be transferred into the Hudson Bay basin as a result of this connection. Information on the biology and distribution of these was collected from the literature in order that assessments could be made of the potential impact of these species on indigenous fish in the Hudson Bay watershed.

The various life histories included in this report provide information on habitat and seasonal distribution, spawning sites, spawning seasons and behaviour, sexual maturity, sex ratios, fecundity, early development (including egg and larvae sizes), growth, food habits, parasites and known effects on other fish of the species named above.

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INTRODUCTION

The Garrison Diversion Project, as proposed in 1976, is a multi-purpose water resource project designed to divert Missouri River water into central and eastern North Dakota where the water will be used to irrigate 250,000 acres of land, provide a municipal and industrial water supply to 14 cities and furnish recreational and fish and wildlife opportunities throughout the area. Figure 1 shows the plan for the Unit and its relationship to Canadian waters.

The Garrison Diversion Project was authorized by the United States Congress as Public Law 89-108 dated August 5, 1965. The Principal Supply Works (Snake Creek Pumping Plant, McClusky Canal, Lonetree Reservoir) for the Unit have been under construction by the U.S. Bureau of Reclamation since 1968.

The Snake Creek Pumping Plant will lift Missouri River water from Lake Sakakawea behind Garrison Dam into Lake Audubon, an impoundment adjacent to Lake Sakakawea. From Lake Audubon the water will flow by gravity through the 73.6 - mile McClusky Canal into Lonetree Reservoir situated on the headwaters of the Sheyenne River near Harvey, North Dakota. Enroute to Lonetree Reservoir the McClusky Canal water will pass through a large screening structure containing two levels of 40-mesh[1] screen designed to prevent the passage of fish, fish eggs and other aquatic life into the reservoir. The 6,515-acre Lincoln Valley Area near the lower end of the McClusky Canal will be served by direct diversions from the canal.

Lonetree Reservoir will be created by construction of

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[1] A 70-mesh screening device has since been proposed for the McClusky Canal.

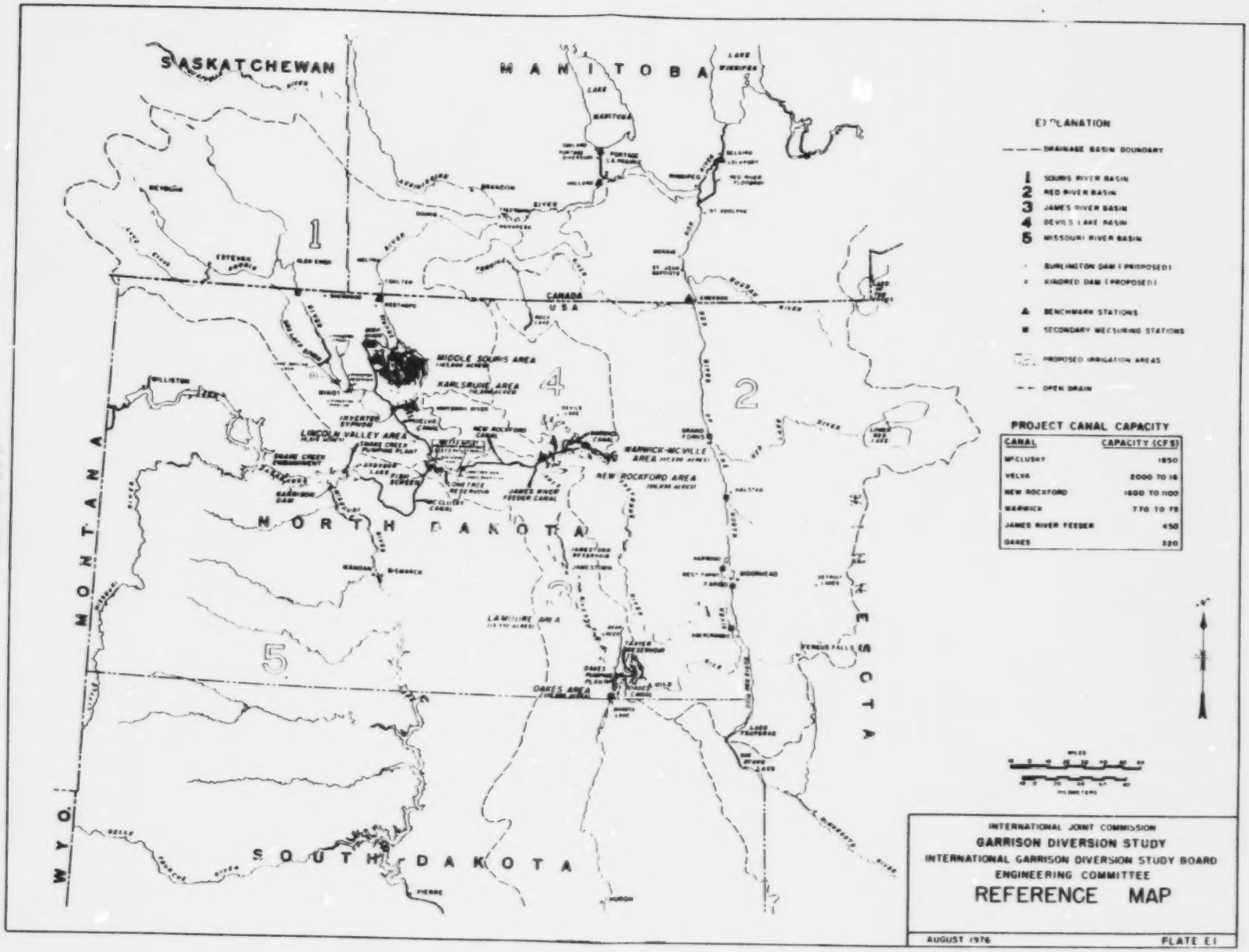

Fig. 1. The Garrison Diversion Unit in North Dakota and its relationship to Canadian waters.

Lonetree Dam on the upper Sheyenne River, Wintering Dam on the headwaters of the Wintering River and the James River Dykes on the headwaters of the James River. The 424,000 acre-foot reservoir is so situated with respect to the topography of North Dakota that water from the reservoir can be diverted by gravity into the Souris, Red and James River Basins as well as the Devils Lake Basin.

The Velva Canal will convey project water northward from Lonetree Reservoir to irrigate the 12,200-acre Karlsruhe Area and 103,800-acre Middle Souris Area. The New Rockford Canal will flow eastward to provide irrigation water for 20,935 acres in the New Rockford Area and to deliver water into the James River Feeder Canal for use in the Oakes - LaMoure Area. The Warwick Canal, an extension of the New Rockford Canal, will serve the 47,220-acre Warwick-McVille Area and provide water for the restoration of the Devils Lake Chain.

Water for the Oakes - LaMoure Area will be diverted from the New Rockford Canal into the James River Feeder Canal leading to the James River near New Rockford. The water will flow down the James River, be re-regulated in the existing Jamestown Reservoir, and continue down the James River. The LaMoure Area (13,350 acres) will be served by a series of small pumping plants along the James River. Water for the 45,980-acre Oakes Area will be pumped from the James River at the Oakes Pumping Plant and flow through the Oakes Canal to Taayer Reservoir, a re-regulation and storage reservoir located on the divide between the East and West Oakes Areas. The irrigable lands will be served by a combination of direct releases from the Oakes Canal and from storage releases from Taayer Reservoir.

As planned, the Garrison Diversion Project involves a transfer

of water from the Missouri River for irrigation, fish and wildlife development and municipal and industrial use in the drainage basins of the James, Souris and Red rivers. A portion of this transferred water will enter the Souris and Red rivers as return flow from irrigated lands, seepage from impoundments and conveyance ditches and as effluent from municipal and industrial waste treatment systems. These flows will then enter Canada mixed with water of the Souris and Red rivers.

The Government of Canada concluded that waters flowing from the Garrison Diversion Project into the Souris and Red rivers in the United States and subsequently into Canada, would cause injury to health and property in Canada and would contravene Article IV of the Boundary Waters Treaty of 1909. Concerns related primarily to the quality and quantity of the water entering Canada and to the introduction of foreign biota.

After a number of discussions between the Canadian and U.S. governments it was agreed to refer the problem to the International Joint Commission for investigation. This was done in October, 1975. The IJC named an International Garrison Diversion Study Board to perform the necessary studies. The Board struck a number of technical committees to gather data on the various problem areas; one of these committees was the Biology Committee.

The Biology Committee[1] devoted considerable time and effort to the problem of introduction of foreign aquatic biota as a result of Garrison. Of particular interest was the assessment of the possibility

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[1] Biology Committee 1976. Biology Committee Report, Appendix C, International Garrison Diversion Study Board Report to the International Joint Commission. 392 pp.

and potential impact of movement of exotic species of fish into the Hudson Bay Basin via the Garrison Diversion Project from the Missouri River Basin. As part of this assessment the Committee arranged to have a number of literature reviews performed on species that were considered to be "problem species" if transferred to the Hudson Bay watershed. These reviews served as the primary information based upon which the Biology Committee made its assessment of the potential impact of introduction of these problem species.

The literature reviews were focussed on a number of points: (1) Did these problem species live or could they occur in areas that would enable them to move into and through the Garrison Diversion Project area into the Hudson Bay watershed? (2) Could they move through the interconnection? (3) Could they survive and establish in the Hudson Bay watershed? (4) What kinds of interactions would occur between exotic and indigenous fishes?

The Biology Committee identified the rainbow smelt, gizzard shad, paddlefish, shovelnose and pallid sturgeons and shortnose gar as "problem species" warrenting literature reviews. The following are these reviews.

THE BIOLOGY AND DISTRIBUTION OF THE ATLANTIC RAINBOW SMELT

is an indication of the great powers of dispersal of this species. Smelt first appeared in Lake Michigan in 1923 near the outlet of Crystal Lake and had dispersed as far as Michigan City at the southern tip of Lake Michigan by 1931 (Van Oosten 1937). Smelt were first reported in the north and south ends of Lake Hurson in 1925 and 1932, respectively (Dymond 1944). Smelt reached Lake St. Clair and eastern Lake Erie by 1932 and 1935, respectively (Dymond 1944). In 1930, smelt were first reported in Whitefish Bay in eastern Lake Superior (Van Oosten 1937). In 1946, they were first noted at the extreme west end of Lake Superior, at Duluth (Hale 1959). Smelt were first reported in Lake Ontario in 1931 (Dymond 1944), probably invading the lake from New York State waters via the Cayuga Lake - Cross Lake - Seneca River - Oswego River route (Scott and Crossman 1973). Since its spread through the Great Lakes, smelt has invaded many other inland lakes of Ontario via unauthorized introductions. They are now known to occur in many lakes of the Parry Sound-Muskoka region including Lake Simcoe and in Eva Lake in the Rainy Lake basin (Scott and Crossman 1973).

The capture of smelt in Kennedy Lake, Itasca County in March, 1959, is the first record of the species from an inland Minnesota lake (Johnson 1963). Smelt were also illegally introduced prior to 1960 into a lake in Pine County, Minnesota, where they are maintaining a moderate population (Swenson 1973). Swenson (1973) indicated that smelt were discovered in the early 1960's in West Bearskin Lake, Cook County and have since spread upstream to Hungry Jack Lake and presumably downstream to Daniels and Rose lakes on the Minnesota-Ontario border. Smelt also occur in Devilfish Lake, Cook County and Burntside Lake, St. Louis County (Swenson 1973).

Introduction

The original range of the Atlantic rainbow smelt, *Osmerus mordax* (Mitchill), in eastern North America was restricted to the Atlantic coastal drainage from about New Jersey to Labrador, where it occurred in both anadromous and landlocked populations (Scott and Crossman 1973). Its range in the inland waters of North America was greatly extended during this century as a result of introductions into the Great Lakes watershed. The effects of the introduced smelt on native fishes in these waters is a matter of controversy. They have been implicated as a factor influencing the decline of several native species, notably the lake herring.

About 1972, smelt were successfully stocked in Lake Sakakawea in North Dakota and the species is now considered to be a part of the Missouri River fauna (Steucke, personal communication, 1976). Smelt does not occur in Manitoba, but may potentially invade the province from Eva Lake in the Rainy Lake basin of Ontario via the Winnipeg River or from the Missouri River watershed via the Garrison Diversion Unit.

This paper describes the known distribution of smelt in North America, summarizes its life history in freshwater and discusses the inter-relationships between smelt and other freshwater fish species.

Distribution of Smelt in North America

Anadromous and indigenous landlocked populations of smelt occur in eastern North America from New Jersey to Labrador (Scott and Crossman 1973). The establishment of smelt in the Great Lakes probably resulted from a planting in Crystal Lake, Michigan, in 1972 (Van Oosten 1937). The spectacular dispersal of smelt throughout the Great Lakes

In North Dakota, smelt were stocked in Lake Sakakawea about 1972 and have been recovered from the lake and the Missouri River south to Lake Oahe (Steucke, personal communication, 1976).

The Life History of Freshwater Smelt

Habitat and seasonal distribution - Freshwater smelt are generally considered to be coldwater fishes, thriving best in oligotrophic waters. Greene (1930) observed that smelt apparently avoid water warmer than 15°C (59°F), except for periodic ventures into surface waters on calm summer evenings. Galligan (1962) found that smelt in Cayuga Lake occurred chiefly below the 55°F isotherm. Hart and Ferguson (1966) suggested that most smelt in Lake Erie occupied water of about 45°F (7.2°C) although they would briefly enter 60°F (15.6°C) water. Johnson (1963) noted that in mid-summer smelt were restricted to regions of the thermocline and hypolimnion in Kennedy Lake where water temperature was 55°F or less.

While a preference for cold water environments may generally exist, other evidence indicates that freshwater smelt are not at all confined to this type of habitat. Rupp (1959) noted smelt populations in 51 of 327 typical warmwater lakes surveyed in Maine. Of the lakes supporting smelt populations, one had a maximum depth of only 14 feet and eighteen did not display thermal stratification although summer temperatures sometimes exceed 70°F (Rupp 1959). MacCallum and Regier (1970) noted that smelt in Lake Erie, especially the yearlings, appeared relatively eurythermic.

Scott and Crossman (1973) stated that smelt "do not inhabit the flowing waters of streams or rivers except at spawning time." However, there is at least one exception to this rule. Rupp (1959) recorded the

early summer occurrence of nonspawning smelt in the outlet stream of Duck Lake, Maine.

The distribution of smelt within lakes varies with age group. Dryer (1966) reported that most 0- and I-group smelt in the Apostle Island region of Lake Superior were taken at depths less than 10 fathoms while the greatest concentrations of smelt aged II and older occurred between 10 and 29 fathoms. Greene (1930) indicated that young smelt were generally found inshore in Lake Champlain in 3 to 4 feet of water until mid-June when they moved offshore to depths of 10 feet or more. MacCallum and Regier (1970) found that by the end of June, young-of-the-year smelt in Lake Erie moved offshore from spawning areas to waters as deep as 15m. In mid-August, after oxygen deficiencies had developed in the hypolimnion, young-of-the-year smelt were captured in the thermocline in Lake Erie (MacCallum and Regier 1970). Ferguson (1965) concluded that young-of-the-year smelt in Lake Erie frequented shallow epilimnial waters, at times becoming greatly concentrated near shore, and did not occur in the hypolimnion. In early spring most yearling smelt in Lake Erie occur in waters 18 m or more in depth (MacCallum and Regier 1970). During the summer, most yearlings in Lake Erie were caught in the hypolimnion or thermocline (MacCallum and Regier 1970). Dryer (1966) found that in Lake Superior's Apostle Island region smelt aged II and over appeared to move offshore in the summer and return to shallower water in the fall. During the summer, smelt appeared to move off the bottom, with concentrations observed 8 fathoms below the surface in 22 fathoms of water (Dryer 1966). Scott and Crossman (1973) indicated that smelt are especially sensitive to light and Ferguson (1965) noted that, in Lake Erie, most smelt were near the bottom at depths of 80 feet or more during daylight hours. Bur-

bidge (1969) observed that in Gull Lake, Michigan, smelt of ages I to V were confined to the hypolimnion and lower regions of the thermocline in summer. Johnson (1963) reported a similar situation in Kennedy Lake, Minnesota. Galligan (1962) noted that in Cayuga Lake greatest smelt densities in summer occurred between depths of 100 and 120 feet and that in the fall smelt moved inshore, occupying depths between 20 and 150 feet in winter, with most of the fish concentrated near a depth of 45 feet. In Gull Lake, Michigan, smelt of all ages are fairly evenly distributed between the surface and depths up to 28 m in fall and winter (Burbidge 1969). MacCallum and Regier (1970) suggested that the spatial distribution of smelt is affected by a complex interaction of factors rather than a simple temperature preference.

Spawning sites - Smelt runs are known from most types of natural lotic environments, from the largest rivers to the smallest temporary brooks (Rupp 1959). Smelt may spawn in streams entering a lake directly, may pass through extensive marshy deadwaters to spawn in areas farther upstream, or may spawn in the deadwater itself (Rupp 1959). Rupp (1959) noted that stream source has no apparent influence since runs occur in lake outlets, upland streams and streams draining extensive swamps and in clear to highly colored waters. Baldwin (1950) suggested that runs appeared heavier in streams with greater currents at their mouths. Runs usually do not ascend rapids (Langois 1935, Baldwin 1950, Hale 1959). While clean gravel or coarse sand may be the preferred stream substrates, eggs have been found deposited in streams on sand, boulders, mud, aquatic vegetation, brush, flooded grasslands, concrete or wood sluicebeds, and on all types of debris (Rupp 1959).

Freshwater smelts also spawn on shoals or beaches in lakes

(Lievense 1954, Rupp 1959). At Branch Lake, Maine, preferred shore-spawning substrates appear to be clean sand or fin gravel, although rubble, coarse gravel, aquatic vegetation, submerged bushes, and debris are also used (Rupp 1959). Rupp (1959) found all shore-spawned eggs in Branch Lake in small patches measuring about 10 by 20 feet, at depths ranging from a few inches to about 2 feet.

The time and site of smelt spawning is unknown in many Maine lakes, suggesting possible further variation in smelt spawning habits (Rupp 1959). MacCallum and Regier (1970) noted that commercial fishermen reported deep-water spawning by smelt at depths of 9 to 22 m in the Long Point area of Lake Erie.

Spawning season - Freshwater smelt are generally cited as being late winter or early spring spawners. Langois (1935) and Hoover (1936) found that the smelt runs at Crystal and Winnesquam lakes, respectively, began when ice disappeared from the surface of the lake. Kendall (1927) gave spawning dates ranging from February through May for 16 Maine lakes. Van Oosten (1940) reported that Great Lake smelt runs began between March 17 and April 28 and ended between March 31 and May 7, and considered the timing to depend on weather conditions, especially water temperature. Rupp (1959) noted a relationship between the times of most smelt runs in Maine lakes and ice-out, indicating that 80% of the runs were in progress within the first 10 days after ice-out (see Figure 2). However, Rupp (1959) also indicated a large variation in the timing of runs, with runs beginning as early as 55 days before ice-out and as late as 19 days after ice-out and ending as early as 40 days before and as late as 31 days after ice-out. The duration of the runs in Maine lakes varies from 1 to 28 days and averages 10 days (Rupp 1959).

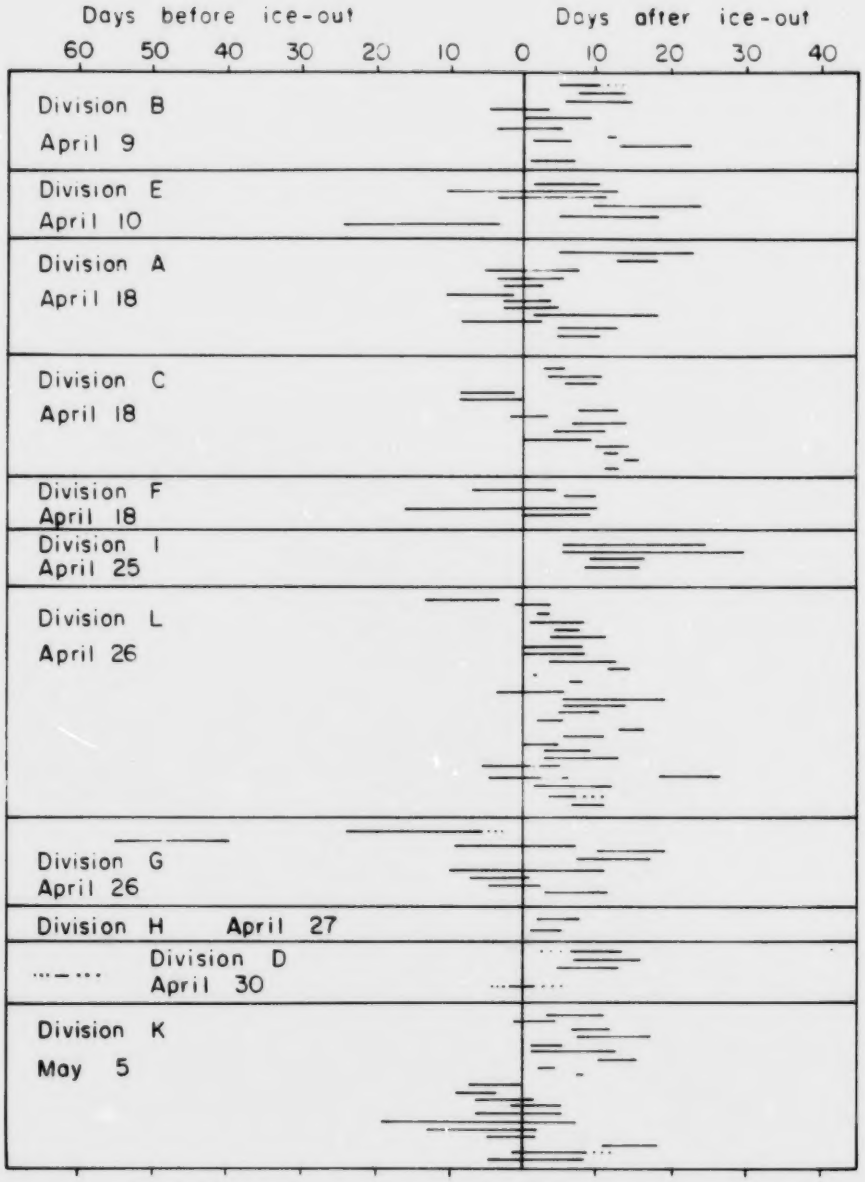

Figure 2. Time and duration of smelt runs in 114 Maine lakes during the season of 1958. The horizontal lines represent the beginning duration, and end of each run with respect to the date of ice-out for each lake represented. Dotted segments of the lines indicate uncertain beginning or ending dates. The Warden Service Divisions which reported these data are arranged according to advancing median date of ice-out for the Division (from Rupp 1959).

Releasing mechanism for spawning - Many authors attempt to show a relationship between the initiation of spawning and stream temperatures, generally citing average temperatures between 40 and 45°F (Rupp 1959). Scott and Crossman (1973) stated that in the Great Lakes watershed spawning runs do not occur until water temperature rises to at least 48°F (8.9°C) or continue after it exceeds 65°F (18.3°C). However, Hoover (1936) observed spawning runs associated with a wide range of temperatures (35.6 to 59°F). Hale (1959) noted that the smelt spawning runs near Duluth began at water temperatures of 35°F or more and that the peaks of the run were associated with water temperatures between 36 and 52°F. Rupp (1959) concluded that lake and stream temperatures alone are not very important in the initiation of smelt spawning runs.

Rupp (1959) suggested that the reproductive behaviour of smelt may be released by the cumulative action of heterogenous stimuli, postulating internal reproductive motivation operating to make the smelt increasingly sensitive to variation in such factors as daily light ration, water temperature, water chemistry, social releasers and sign stimuli received in the spawning area. Rupp (1965) concluded that intragroup stimulation dependent upon the overall density of smelt in a spawning school and/or the presence of a certain critical proportion of females is probably the main factor operating in the release of the spawning act.

Description of spawning runs - Smelt are usually cited as nocturnal spawners (Langois 1935, Hoover 1936, Scott and Crossman 1973), with the fish drifting back to the lake by day (Langois 1935) or during the night after the peaks of each run (Hoover 1936). Some spawners, mostly

males, remain in the streams throughout the day (Langois 1935, Hoover 1936, Baldwin 1950). Rupp (1959) noted a few cases of daytime spawning.

Rupp (1959) observed that the time of night runs varied from immediately to several hours after nightfall, with all runs beginning by 12:30 a.m. at the latest. Hoover (1936) indicated that the runs from Winnisquam Lake peaked twice each night, once between 10:00 and 11:00 p.m. and again between 12:00 M. and 1:30 a.m. Rupp (1959) indicated that smelt may not run every night during the spawning period and noted evidence of a possible inhibitory effect of storms and bright moonlight and of the operation of other unknown controlling factors not associated with weather.

The sex ratio of the runs shifts from a predominance of males in runs early in the spawning season to a predominance of females later in the season (Langois 1935, Hale 1959, Bailey 1964). Bailey (1964) observed equal proportions of males and females during the peak of the spawning season. Hoover (1936) and Hale (1959) reported great fluctuation in the sex ratio during a single night's run. Hoover (1936) indicated that spawning began when the ratio of males to females was about 4 to 1 and increased in intensity as the ratio became more nearly equal.

Creaser (1925) and Schneberger (1937) reported spawning at age II at total lengths of 6.5 to 7.5 and 6.5 to 8.5 inches in Crystal Lake and Green Bay, respectively. Warfel *et al.* (1942) and Hale (1959) found age II males and females dominating spawning runs from Great Bay, New Hampshire and at Duluth, respectively, with age III fish the next most abundant group. Bailey (1964) observed the reverse situation in western Lake Superior. Baldwin (1950) noted that the smelt in spawning

runs in South Bay, Lake Huron, average 5.7 inches (145 mm) in fork length and 0.73 ounces (20.6 gm) in weight. At Duluth, spawning males and females ranged from 4.5 to 7.4 and 4.5 to 10.4 inches in total length, respectively (Hale 1959). Bailey (1964) indicated that both the average length and age of spawning smelt of both sexes apparently decrease as the spawning season progresses.

Schneberger (1937) indicated that smelt apparently do not feed during spawning runs but Baldwin (1950) found evidence of moderate feeding, mainly on mayfly numphs, during the spawning period.

Scott and Crossman (1973) described smelt spawning in streams. Two or more tuberculated males maintain positions against a single female in the current. The eggs are released in clusters and presumably the milt is released simultaneously. The eggs become adhesive shortly (15 to 20 seconds) after extrusion and attach to the bottom via their adhesive outer coat. The outer coat is stripped off the egg by the current except at a single point of attachment where it forms a stalk or holdfast.

Sexual maturity - Bailey (1964) found that smelt in Lake Superior were all immature after one growing season and all mature after three or more growing seasons. He noted that 40.7% of males and 17.7% of females matured after two growing seasons and concluded that many Lake Superior smelt thus do not reach maturity and spawn at age II. However, Hale (1959) found that the 1954 spawning run at Duluth in Lake Superior was predominantly age group II, as mentioned above. Greene (1930) reported that the small race of smelt in Lake Champlain matured at 2 winters but that only about one-third of the larger race matured at this age.

Bailey (1964) found that all smelt under 5.0 inches long were immature and that the shortest mature male and female caught in western Lake Superior were both in the 5.0 - 5.2 inch length interval. Bailey (1964) concluded that males were first to reach 100% maturity, noting that all males were mature at the 5.9 - 6.1 inch length interval, but that an immature female occurred in the 6.5 - 6.7 inch interval. He indicated that over 50% of the females were mature at the 5.6 - 5.8 inch interval and all were mature at the 6.8 - 8.0 inch interval.

Sex ratio - Beckman (1942), Bailey (1964) and Burbidge (1969) reported a predominance of females in smelt populations in Crystal Lake, Lake Superior and Gull Lake, respectively, citing percentages of 61, 68 and 60, respectively, for the proportions of females in these populations. They also observed an increase in the proportions of females with age, suggesting a differential mortality between the sexes. Burbidge (1969) suggested that a greater mortality among males may result from their more active and prolonged spawning activity.

Fecundity - Fecundities reported for smelt are summarized in Table 1. Scott and Crossman (1973) suggested that fecundity increases with the size of the female smelt. However, Bailey (1964) found no clear relationship between fecundity and size. Bailey (1964) calculated that Lake Superior smelt contained an average of 14,673 eggs per ounce of female.

Table 1. Fecundity of smelt.

Author	Location	Length of female		No. of eggs per female	Average fecundity (eggs/female)
		Inches	mm		
McKenzie (1964)	Miramichi R.	5.0 - 8.2	127-209	8500-69,600	-
Baldwin (1950)	South Bay, L. Huron	5.5 - 7.5	140-190	9650-26,800	-
Van Oosten (1940)	Great Lakes	4-9	102-229	1700-43,125	-
Bailey (1964)	Western L. Superior	7.3 - 8.8	185-224	21,534-40,894	31,338
Langois (1935)	Crystal L.	7.2 - 7.6	185-195	-	25,102
Langois (1935)	Crystal L.	9.0	232	43,125	-

Early development and growth - Bailey (1964) reported mean egg diameters ranging from 0.79 to 0.99 mm and averaging 0.86 mm for smelt in western Lake Superior. He found no relationship between egg diameter and fish size. Schneberger (1937) found that 73.6% of 962 eggs collected in Green Bay contained developing embryos. Rothschild (1961) estimated egg survival to the prehatching stage to be 24% in Dean Brook, Maine. Estimates of survival-to-hatching of smelt eggs at shore-spawning sites in Branch Lake, Maine, ranged from virtually zero (0.027%) to just over 2%, with a weighted average survival of about 1.06% (Rupp 1965). McKenzie (1947) observed hatching successes in enclosed stream areas ranging from 0.05 at a very high egg density (54,000 eggs/sq. ft.) to 3.70% at a low density (487 eggs/sq.ft.). Optimum egg density in McKenzie's (1947) study appeared to be between 6000 to 15000 eggs/sq.ft., yielding hatching successes of about 1.8 and 0.8%, respectively (Rupp 1965). Rupp (1965) concluded that the mean survival of shore and stream-spawned eggs does not differ greatly, implying that shore spawning imputes no intrinsic disadvantage to eggs laid. Probable causes of mortality among shore-spawned eggs include the grinding actions of surf, declining water levels, and trampling (Rupp 1965). The hatching times reported for smelt eggs are listed in Table 2.

Smelt are about 5 mm long when hatched, measure 20 to 40 mm in length within a few months of hatching and may be up to 2 inches (51 mm) long by August (Scott and Crossman 1973). The average lengths and weights of smelt are given by age group for a number of North American lakes and rivers in Tables 3 and 4. Growth rates shown by

Table 2. Time to hatching of smelt eggs.

Author	Location	Hatching Time (days)	Temperature (^{o}F)
Hoover (1936)	Winnisquam Lake	10	50 - 62 (average 58.9)
Hale (1959)	L. Superior(hatchery)	19 - 20	35 - 67 (mean daily high and low, 47 and 41)
McKenzie (1964)	Miramichi R.	29	42.8 - 44.6
		25	44.8 - 46.4
		19	48.2 - 50.0

Table 3. Average total lengths in inches and millimeters (in parentheses) of smelt in different age groups. Figures are for fish captured in late winter or spring except for Burbidge's data which were collected between December and November.

Author	Location	Sex	Age (years)						
			0	I	II	III	IV	V	VI
Creaser (1925)	Crystal Lake	Combined	-	-	6.5-7.5 (165-190)	9(229)	10(254)	10.75-12 (273-305)	-
Schneberger (1937)	Green Bay	Combined	-	-	7(179)	10(254)	12(305)	14(356)	-
Beckman (1942)	Crystal Lake	Combined	-	4 3/8(111)	7(179)	7 3/4(197)	8¼(210)	-	-
Warfel *et al.* (1942)	Great Bay	Combined	-	3.38(86.0)	5.70(144.8)	6.73(171.0)	8.70(220.0)	-	-
Burbidge (1969)	Gull Lake	Combined	2.3(60.2)	5.8(149.8)	6.4(163.2)	7.0(180.2)	7.7(197.7)	7.3(186.5)	-
Zilliox & Youngs (1958)	Lake Champlain	Male	-	6.4(162.0)	8.2(208.8)	9.4(238.6)	10.7(271.3)	11.3(287.5)	-
		Female	-	6.4(163.8)	8.4(213.5)	10.0(253.0)	10.9(276.4)	11.7(298.2)	-
Bailey (1964)	Lake Superior	Male	-	2.6*(66)	6.0(152)	7.3(185)	7.9(201)	8.6(218)	
		Female	-	2.6*(66)	5.9(150)	7.7(196)	8.7(221)	9.4(239)	9.8(249)
McKenzie (1964)	Miramichi River	Male	-	-	5.3(135)	6.0(152)	6.7(169)	7.2(183)	-
		Female	-	-	5.5(139)	6.3(160)	7.2(183)	8.1(206)	-

*Sexes combined.

Table 4. Average weights in ounces and grams (in parentheses) of smelt in different age groups. Figures are for fish captured in late winter or spring except for Burbidge's data which was collected between December and November.

Author	Location	Sex	Age (years)						
			0	I	II	III	IV	V	VI
Warfel *et al.* (1942)	Great Bay	Combined	-	0.0864 (2.45)	0.59 (16.73)	1.07 (30.62)	1.94 (55.0)	-	-
Burbidge (1969)	Gull Lake	Combined	0.049 (1.4)	0.81 (22.9)	0.97 (27.6)	1.41 (40.1)	1.75 (49.6)	1.33 (37.8)	
Bailey (1964)	Lake Superior	Male	-	-	0.7 (19.8)	1.4 (39.7)	1.9 (53.9)	2.3 (66.1)	
		Female	-	-	0.7 (19.8)	1.7 (48.2)	2.5 (70.9)	3.2 (90.7)	3.8 (107.7)

smelt in different lakes are highly variable. Greene (1930) reported the occurrence of two races of smelt in Lake Champlain. The lengths attained by the larger race are shown in Table 3. The average length of the oldest age group of the small race was only 160 mm (6.3 inches) (Zilliox and Youngs 1958). Smelt from Crystal Lake (Creaser 1925), Green Bay Schneberger 1937), Lake Superior (Bailey 1964), Great Bay (Warfel *et al.* 1942), and Lake Champlain (Zilliox and Youngs 1958) all grew faster than Gull Lake smelt, possibly due to dissimilar diets (Burbidge 1969). MacKay (1963) noted very rapid growth in Lake Erie, where two year olds are 8.1 to 9.4 inches long and weigh 2½ to 3 3/4 ounces. Females tend to be larger than males in the older ages and the difference in size between the sexes increases with age (Warfel *et al.* 1942, Zilliox and Youngs 1958, Bailey 1964). However, Burbidge (1969) found little difference in size between the sexes. The greatest growth in length occurs in the first year (Warfel *et al.* 1942) or the second year (Bailey 1964, Burbidge 1969). Bailey (1964) found the best growth in weight in the third year. Scott and Crossman (1973) stated that in small inland lakes smelt often attain a maximum length of about 4 inches (102 mm) but in Lake Ontario and marine coastal waters smelt as long as 14 inches (356 mm) have been taken. Kendall (1927) reported average lengths ranging from 2.3 to about 12 inches in 21 Maine lakes and recorded a smelt 15.75 inches in total length. Rupp (1959) indicated that the usual size of smelt in Maine waters is between 4 and 8 inches, total length.

Food habits - Table 5 summarizes the food habits of smelt

Table 5. Food habits of freshwater smelt.

Author	Location	Item	Frequency of occurrence (%)	% of food volume	Other remarks
Schneberger (1937)	Green Bay, L. Michigan	*Mysis relicta*	75		Other items eaten: amphipods, fingernail clams, *Hexagenia*, dipterous larvae, oligochaetes, fish
Baldwin (1950)	South Bay Lake Huron	*Mysis* dipterous larvae sculpins	86 12 9		Samples taken in summer. Also ate a few mayfly nymphs, caddisfly larvae and ostracods.
Gordon (1961)	Saginaw Bay Lake Huron	crustaceans (mainly *Mysis* cladocerans) insects (mostly *Hexagenia*) fish (smelt, young *Notropis*)	71 31 8	36 44 20	Fish aged I and older
Johnson (1963)	Kennedy Lake	Cladocerans, copepods Chironomid and *Chaoborus* larvae	94 59	58.6 41.4	Samples taken in summer. Fish aged I and over single oligochaete and mayfly nymph also found
Hale (1959)	Lake Superior	*Mysis*	75-89.1	82.4	Fish < 6" total length. Amphipod *(Pontoporeia sp.)* also important
		Mysis *Pontoporeia* fish (mostly YOY smelt)	8-15.4	49.7 16.5 28.6	Fish 6.0 - 13.0 inches total length

in several lakes in North America. MacKay (1963) stated that plankton was the first food taken by young smelt, that insect larvae and crustacea were later taken, and that fish, mainly other smelt, were finally eaten at lengths of 6 inches or more. In most populations, juvenile smelt feed primarily on small crustaceans, mainly copepods and cladocerans (Kendall 1927, Greene 1930, Gordon 1961). In the Great Lakes, adult smelt feed primarily on *Mysis relicta*, with other crustaceans, usually copepods or amphipods, being second in importance (Schneberger 1937, Baldwin 1950, Hale 1959, Anderson and Smith 1971a). Gordon (1961) found that cladocerans and insects, mainly mayfly larvae, were major items in the diet of smelt of age I and over in Saginaw Bay, Lake Huron. Scott and Crossman (1973) stated that fish comprised 6 to 10% of the food volume of older smelt and that sculpins and small smelt were the most common fish eaten in the Great Lakes, although small burbot white bass, whitefish and emerald shiners were also reported. Hale (1959) identified 3 trout from the stomachs of smelt from Lake Superior. Creaser (1925, 1927) found that smelt in some inland Michigan lakes fed on young perch, lake shiners and rock bass. Adult smelt in New England lakes sometimes feed exclusively on young-of-the-year smelt (Greene 1930). Anderson and Smith (1971a) found small amounts of smelt and coregonid eggs in the stomachs of large smelt in Lake Superior between April and June.

Burbidge (1969) noted a seasonal variation in the diet of smelt in Gull Lake, Michigan. *Chaoborus* larvae were

a common food item throughout the year in Gull Lake but were most common in the summer. Chironomid larvae were of major importance in the summer only. Cladocerans and copepods were frequent items in the fall, winter and spring. Burbidge (1969) indicated that this seasonal variation in diet suggests that the most available or abundant suitable fauna are preyed upon by smelt.

Burbidge (1969) noted that the diet of Gull Lake smelt is unusual in that it consisted primarily of small crustaceans and dipteran larvae all throughout life, with no switch to fish or large invertebrates such as *Mysis* by older smelt. He concluded that this less efficient diet resulted in the relatively slow growth rates of Gull Lake smelt. A similar diet occurs in Kennedy Lake, Minnesota, in the summer (Johnson 1963). Lackey (1969) reported a diet of plankton, insects and isopods for smelt in Echo Lake, Maine.

Parasites - The microsporidian parasite, *Glugea hertwigi* Weissenberg, has been reported in smelt in Lake Erie and many parts of Quebec (Scott and Crossman 1973). In Loon Pond, New Hampshire, it caused an acute epidemic of microsporidiosis in the fall of 1951 (Haley 1952). This parasite is aesthetically undesirable but is not known to be a human pathogen (Scott and Crossman 1973). Bangham (1955) found that all 50 smelt he examined from Lake Huron were parasitized with acanthocephalans or numerous flukes *(Diplostromulum sp.)* in the lenses of the eyes. Hoffman (1967) listed a number of species of trematodes, cestodes, nematodes and

acanthocephalans and *Piscicola punctata* (a leech), *Argulus alosae* and *Glugea hertwigi* as the parasites of the American smelt.

Effects of smelt on other fish - The effects of smelt introductions on native fish stocks is a matter of controversy. Smelt have been implicated as a factor contributing to the declines of lake herring, whitefish, deepwater cisco, lake trout, walleye and blue pike in the Great Lakes but evidence for this is mostly circumstantial. Anderson and Smith (1971a) concluded that the introduction and subsequent increase in the abundance of smelt in Lake Superior has undoubtably had a definite effect on the endemic species, as evidenced by the predominant percentage use of most food organisms by smelt. Gordon (1961) indicated that in Saginaw Bay, Lake Huron, smelt compete for food with the young of all associated species and the adults of some. However, he noted that adverse effects from smelt competition require a rate of consumption so great that a food scarcity develops and that no evidence of such a food shortage exists in Lake Huron.

Wells and McLain (1973) noted a striking inverse relationship between smelt and lake herring abundance in Lake Michigan, with herring abundance first decreasing as smelt increased in numbers in the 1930's, then increasing strikingly after the catastrophic smelt die-off of 1942-1943, and finally declining disasterously in the late 1950's as smelt regained their former abundance. Anderson and Smith (1971b) observed that the sharp

decline in the lake herring catches in western Lake Superior in the late 1950's coincided with a sharp rise in smelt catches. The ascendency of smelt in the Bay of Quinte in Lake Ontario coincided closely with a collapse of the lake herring population (Christie 1972). Anderson and Smith (1971b) and Wells and McLain (1973) suggested that food competition by smelt, especially with the larval stages, may have been a major factor causing the above lake herring declines. Smith (1972) noted possible evidence of a feeding dominance of smelt over lake herring in Lake Superior. The distributions of smelt and lake herring in lakes Ontario and Superior are quite similar (Wells and McLain 1973, Anderson and Smith 1971b), providing ample opportunity for a competitive interaction. Anderson and Smith (1971b) and Wells and McLain (1973) also suggested that smelt may prey upon young lake herring but noted that no evidence of such predation existed. Anderson and Smith (1971b) noted the occurrence of concentrations of smelt on herring spawning grounds during the spawning season and suggested that successful lake herring spawning may have been impaired by smelt crowding lake herring on the spawning grounds.

The substantial increase in the smelt population in Lake Michigan may have contributed to the marked decline in whitefish abundance in the lake after 1949 (Wells and McLain 1973). Wells and McLain (1973) noted that the phenomenal decline of smelt in the winter of 1942-43 coincided with the production of an unusually successful whitefish year class in the spring of 1943, possibly due to a lack of interference by smelt with whitefish fry. Although not commonly eaten, whitefish has been reported in the stomach contents of smelt (Scott and Crossman 1973). Berst

and Spangler (1972) suggested that the large 1943 whitefish year class in Lake Huron resulted from an increased food supply after the smelt die-off in the winter of 1942-43.

Christie (1972) noted the coincidence of the ascendency of smelt and the collapse of deepwater cisco stocks in Lake Ontario. The summer distribution of deepwater ciscoes is considerably deeper than that of smelt but the former may spawn in water as shallow as 120 ft (37 m), possibly allowing predation on cisco eggs and larvae by smelt (Christie 1972). Anderson and Smith (1971b) reported the occasional occurrence of coregonid eggs in smelt stomachs in Lake Superior in spring.

The relationship between lake trout and smelt is uncertain. Smelt is usually cited as a major food item of adult lake trout (Hale 1959, Dryer *et al.*(1965) also noted that smelt were rare in the stomachs of lake trout caught in Lake Superior at depths greater than 35 fathoms and that they were an important food item of trout caught in shallower water only from February through June. Dryer *et al.* (1965) found that the smallest trout eating smelt in Lake Superior were in the 6.0 - 6.9 inch length interval. Eschmeyer (1956) noted that *Mysis* was the most important food of young lake trout in Lake Superior. Crustaceans, mainly *Mysis* and the amphipod *Pontoporeia*, comprised 70% of the food volume of lake trout 4.0 - 7.9 inches long in Lake Superior (Dryer *et al.* 1965). Since *Mysis* and *Pontoporeia* are among the most important food items of smelt in the Great Lakes, it is

likely that smelt are in direct competition with young lake trout for food. *Mysis* is also a very frequent item in the stomachs of older lake trout caught in Lake Superior at depths less than 35 fathoms (Dryer *et al.* 1965), indicating that smelt may also compete with older trout for food. Although most studies had failed to find any direct evidence of predation by smelt on trout (Scott and Crossman 1973), Hale (1969) did find three trout in the stomach contents of smelt from Lake Superior. Due to their huge numbers, predation by even a very small percentage of a smelt population could be significant (Scott and Crossman 1973). Scott and Crossman (1973) noted that smelt appear to be more piscivorous in winter when few studies are conducted on smelt diets. Also, predation by smelt on trout fry would be difficult to detect due to the rapid digestion of these fragile organisms.

MacCallum and Regier (1970) consistently caught yearling and adult yellow perch associated with smelt in Lake Erie. Perch are known to feed on smelt (MacKay 1963, Scott and Crossman 1973). Conversely, smelt fed on young perch in some inland Michigan lakes (Creaser 1925, 1927). In Saginaw Bay, Lake Huron, immature insects (mainly chironomids and mayflies) are an important food item for all size groups of yellow perch and cladocerans and copepods are eaten in large numbers by smaller perch (Tharratt 1959). Cladocerans and mayfly larvae are major food items of older smelt in Saginaw Bay (Gordon 1961), indicating the possibility of competition between smelt and perch for food.

Regier *et al.* (1969) and Hartman (1973) proposed that smelt may have been influential in the severe walleye decline in Lake Erie after 1957. Wells and McLain (1973) noted that an extremely strong walleye year class followed the smelt die-off in Lake Michigan in the winter of 1942-43. Walleye spawning runs to areas adjacent to the central basin of Lake Erie may have failed due to excessive predation by yearling smelt upon pelagic walleye fry (Regier *et al.* 1969). Since the initial food source of walleyes in Oneida Lake is large zooplankton, especially copepods (Houde 1967), smelt may compete with young walleyes for food. Older walleyes, however, are known to feed on smelt (Scott and Crossman 1973). Forney (1965) found that walleye production in Oneida Lake was closely correlated to the abundance of young yellow perch. Thus, if smelt prove to have a detrimental effect upon perch populations, they will also indirectly affect walleye production.

Summary

The Atlantic rainbow smelt occurs in eastern North America from about New Jersey to Labrador, in the Great Lakes watershed, in several inland lakes in Minnesota and Ontario, and in Lake Sakakawea and the Missouri River in North Dakota.

Although generally considered to be coldwater fishes, thriving best in oligotrophic waters, smelt also occur in numerous warmwater lakes. Smelt usually occur chiefly below the 55°F isotherm in summer and appear to avoid water above 59°F.

However, MacCallum and Regier (1970) found Lake Erie smelt to be relatively eurythermic. Although exceptions exist, nonspawning smelt usually do not inhabit streams or rivers.

Young smelt occur inshore until mid- to late June. By the end of June, young-of-the-year smelt move offshore to water as deep as 15 meters. During the summer, adult smelt appear to move offshore and off the bottom. In stratified lakes, smelt are apparently confined to the hypolimnion and lower regions of the thermocline in summer. Smelt move inshore in the fall.

Smelt spawn in all types of natural lotic environments and on shoals or beaches in lakes. Gravel and sand are the preferred spawning site substrates, although a wide variety of other substrates are also used. In Maine, most spawning runs are in progress within the first 10 days after ice-out. However, a large variation occurs in the timing of runs, which may start as early as 55 days before and as late as 19 days after ice-out. Maine runs average 10 days in duration. Smelt spawning runs are associated with a wide range of water temperatures (about 35 to 59°F). The reproductive behavior of smelt might be released by the cumulative action of heterogenous stimuli or intragroup stimulation. Smelt usually spawn at night, although exceptions occur. The sex ratio of runs shifts from a predominance of males early in the spawning season to a subsequent predominance of females. The sex ratio may fluctuate

greatly during a single night's run. Spawning runs are dominated by fish or age II or III, the ages at which smelt first mature. Males reach 100% maturity at a shorter length than females. Females are predominant in nonspawning populations, suggesting differential mortality between the sexes. Reported fecundities of smelt range from 8500 to 69,600 eggs per female.

The diameter of smelt eggs ranges from 0.79 to 0.99 mm. Survival-to-hatching to shore-spawned eggs averages about 1%. Hatching success of stream-spawned eggs is about 0.8 to 1.8% at optimum egg densities (between 15,000 and 6000 eggs/sq.ft.). Hatching times reported for smelt eggs range from 10 days or less (at 50 to 62°F) to 29 days (at 42.8 - 44.6°F).

Smelt are about 5 mm long when hatched and may be up to 51 mm long by August. Growth rates are highly variable among smelt in different lakes, possibly due to varying diets. Females usually tend to be larger than males in the older ages. The usual length of smelt in Maine waters is between 4 and 8 inches, although fish up to 15.75 inches long have been captured.

Juvenile smelt feed primarily on small crustaceans, mainly copepods and cladocerans. In the Great Lakes, adult smelt feed primarily on *Mysis relicta*, although copepods, amphipods, cladocerans and mayfly larvae are also important food items. Older smelt also feed on fish, usually sculpins and small smelt, although small burbot, white bass, rock bass, yellow perch, emerald shiners, whitefish and trout

have also been reported from smelt stomachs. Isopods and chironomid and *Chaoborus* larvae are also important food items in some lakes.

Smelt are parasitized by a number of species of trematodes, cestodes, nematodes and acanthocephalans and *Piscicola punctata* (a leech), *Argulus alosae* and *Glugae Hertwigi*.

Smelt have been implicated as a factor contributing to declines of populations of lake herring, whitefish, deepwater ciscoes, lake trout, walleye and blue pike. Several authors have noted inverse relationships between the abundances of lake herring, whitefish and deepwater ciscoes and that of smelt in the Great Lakes. Smelt may compete for food with lake herring, whitefish, yellow perch, young walleye and young lake trout and, to a lesser degree, older lake trout. Smelt may also prey on the eggs and young of lake herring, whitefish, deepwater ciscoes, perch, walleye and lake trout but there is little direct evidence for this. Smelt may interfere with successful lake herring spawning by crowding the herring on their spawning grounds. Smelt are eaten by older lake trout, yellow perch and walleye.

LIFE HISTORY OF THE GIZZARD SHAD

Introduction

The gizzard shad, *Dorosoma cepedianum* (Le Sueur), occurs in the waters of the Atlantic slope from southern New York, south to the Gulf coast of the United States, and to the basin of the Rio Panuco in eastern Mexico (Miller 1960). Inland, the species ranges from southeastern South Dakota and central Minnesota, the Great Lakes drainage, southern New York, and throughout the Mississippi valley (Scott and Crossman 1973). It also occurs in the Rio Grande drainage in Mexico, New Mexico drainages east of the Continental Divide, eastern Colorado and eastern Wyoming (Jester and Jensen 1972). Carufel and Witt (1963) noted the occurrence of gizzard shad in North Dakota. The species has extended its range via migrations through manmade canals. It first entered Lake Michigan via the Chicago River Canal and the Erie Canal may be responsible for its presence in northern Cayuga Lake, New York (Miller 1956).

The role of the gizzard shad in the ecology of fish populations is difficult to assess. When small, the shad is undoubtably an important food of game fishes. However, because of its high reproductive potential and rapid growth rate, it tends to overpopulate many waters to the detriment of other fish populations (Jester and Jensen 1972). Bodola (1966) questioned whether the value of shad in Lake Erie as forage is outweighed by its diversion of the productive capacity of the lake into commercially valueless fish.

This paper summarizes the life history of the gizzard shad. This information will aid in a critical assessment of the role of this species in freshwater ecosystems.

The Life History of the Gizzard Shad

Habitat and movements - The gizzard shad inhabits large rivers, reservoirs, lakes, swamps, bays, borrow pits, bayous, estuaries, temporary floodwater pools, sloughs and similar quiet open waters which may be clear to very silty (Miller 1960). It is fairly common in the relatively strong current of the upper Mississippi River but prefers the quieter waters downstream (Miller 1960). In coastal regions, the species frequents brackish waters with salinities from 2.0 to 33.7 parts per thousand and, in general, the smallest fish occur in the freshest water (Miller 1960). In Lake Erie, gizzard shad are most plentiful in the shallow waters around the periphery of the western end of the lake and in the Bass Islands area, especially in protected bays and the mouths of tributaries (Bodola 1966) and over mud bottoms (Nash 1950). Although collected over all types of substrate (mud, sand, gravel, bedrock and inundated vegetation) in Elephant Butte Lake, New Mexico, they were taken most consistently over sand and gravel in shallow water (Jester and Jensen 1972). In Elephant Butte Lake their distribution appeared to be affected by water clarity. Large numbers occurred where Secchi disc visibility was as low as 6 inches (15 cm), but catches decreased at visibilities near 60 inches (152 cm) (Jester and Jensen 1972).

Miller (1960) described the gizzard shad as "essentially an open-water species, usually living at or near the surface". In Elephant Butte Lake, gizzard shad occupy chiefly the littoral and limnetic areas (Jester and Jensen 1972). Jester and Jensen (1972) collected gizzard shad in shallow water during all months, although in reduced numbers from November through March. Gizzard shad apparently move into deeper areas of Elephant Butte Lake and cease activity almost entirely in the fall as water temperature approaches 14°C (57.2°F) and become active and return to littoral areas in the spring as the water warms to 14°C (Jester and Jensen 1972). Jester (1962) caught gizzard shad at depths of 70 and 80 feet (21 and 25 m) during the winter in Conchas Lake, New Mexico. Jester and Jensen (1972) collected gizzard shad in Elephant Butte Lake in profundal net-sets to a depth of 52 feet and in nets set at a mid-depth of 23 feet in 52 feet of water. In Norris Reservoir, Tennessee, gizzard shad have been caught from the surface to a depth of 108 feet (33 m) (Dendy 1945). In the Coosa River, Alabama, they are found in both deep (25 feet) and shallow water (Scott 1951).

In western Lake Erie, young gizzard shad live close to shore in mid-summer, usually in shallow water (Bodola 1966). They apparently prefer beds of spatterdock *(Nuphar)* in Foots Pond, Indiana (Hubbs and Lagler 1943).

In Norris Reservoir, young-of-the-year gizzard shad occur in compact schools soon after hatching, but most schools

disperse by fall and few form the following spring (Dendy 1946a). Schooling largely ceases by the time the fish are a year old in Norris Reservoir (Dendy 1946a). However, Jester and Jensen (1972) first observed young-of-the-year shad in schools in the fall in Elephant Butte Lake. Jester (1962) observed many large schools of shad of all ages in Conchas Lake. All ages of gizzard shad were caught in large numbers in individual nets in Elephant Butte Lake, either indicating schooling or simply reflecting a very high population density (Jester and Jensen 1972).

A spring migration of gizzard shad (apparently a spawning run) has been observed in the Mississippi River near New Orleans (Miller 1960). Adults may ascend small streams and ditches to spawn (Miller 1960). Miller (1960) noted a fall "run" in the Chesapeake Bay region and a corresponding spring "run" in North Carolina. Swanson (1932) noted an unusual mid-winter migration in the Minnesota River from about December 1 until late January. Bodola (1966) found that most ripe males and females migrated from deeper to shallower water during the spawning season in Lake Erie and that spent fish returned to the open lake.

Hart (1952) found that gizzard shad can withstand temperatures up to 35^{o}C and show no geographic variation in their ability to tolerate lethal temperatures. However, information cited below suggests some variation in the shad's tolerance of low temperatures. Brett (1956) reported upper lethal temperatures for gizzard shad of 34.3 and 35.9^{o}C at acclimation temperatures

of 25 and 30°C, respectively. The lower lethal temperatures at the above acclimation temperatures were 10.8 and 14.5°C, respectively (Brett 1956). Jester and Jensen (1972) observed winter mortality of gizzard shad associated with low temperatures in New Mexico lakes. Mortality of young-of-the-year shad was first observed at temperatures below about 3.3°C (38°F). High mortality rates which decimated young age groups and involved older fish were observed by Jester and Jensen (1972) in Caballo Lake at 2.8 - 3.0°C (37 - 37.5°F). High mortality rates were rare in Conchas Lake at temperatures above 2.2°C (36°F) (Jester and Jensen 1972). Miller (1960) described mass mortalities of gizzard shad in Lake Erie and the Miami Canal, Ohio, which probably resulted from sudden temperature rises. In the Lake Erie example, the mortality occurred in the West Basin, in Presque Isle Bay, when water temperature was warmed to 55 to 60°F by discharges from an electric power plant; water temperatures in the rest of the bay were only 34 - 35°F. The absence of mass mortalities in the colder part of the bay suggests that Lake Erie shad may be more tolerant of low temperatures than the shad studied by Jester and Jensen (1972) in New Mexico. Shields (1956) observed the mortality of young shad in the Fort Randall Reservoir, South Dakota, during the winter.

Bodola (1966) found that shad in Lake Erie concentrated in winter in areas near warm inflowing streams and were attracted to

the warmer waters of outlets from industrial plants. Miller (1956) noted that temperature is apparently important in controlling the distribution of gizzard shad. He indicated that shad forge northward during series of warm years but are almost eliminated from the new waters in cold years.

Spawning season - Table 6 summarizes observations on the spawning season of gizzard shad. Gizzard shad spawning occurs as early as March and April in Florida and Alabama and as late as mid-August in Alabama (Swingle 1949, Berry 1955, Moody 1957). In Lake Erie, most gizzard shad spawn in June and early July (Bodola 1966). In Fort Randall Reservoir, all adult shad obtained before June 24, 1955, were green and all those caught after July 6 had spawned, indicating a short and comparatively late spawning period in South Dakota near the northern limit of the gizzard shad's range (Shields 1956). Bodola (1966) noted that in Lake Erie precociously mature I-group shad might spawn in late July or early August after the fish in age groups II and older had completed spawning. Jester and Jensen (1972) described evidence of a second but less pronounced spawning period in late summer in Elephant Butte Lake, New Mexico. Johnson (1971) noted indications that the closely related threadfin shad (*Dorosoma petenense* Günther) spawns more than once a year in southern waters at least. However, he reported that in the Salt River reservoirs of Arizona a second compliment of eggs that older threadfin shad begin to mature appears to be resorbed rather than spawned. Jester and Jensen (1972), however,

Table 6. Spawning season of the gizzard shad.

Source	Location	Dates	Water Temperature
Moody (1957)	L. Panasoffkee, Florida	Most spawning March and April. Spawning completed in May.	-
Berry (1955)	L. Newman, Fla.	Peak spawning April 1	-
Langlois (1954)	North Reservoir, Ohio	May 29	64°F (17.8°C)
Harland and Speaker (1956)	Iowa	Late April or early June	-
Swingle (1949)	Alabama ponds	1941 - hatching from late April to August 20. 1942 - hatching from mid-March through July.	-
Eschmeyer *et al.* (1944)	Chickamauga Reservoir, Tennessee	Late May	-
Dendy (1946b)	Norris Reservoir, Tennessee	1943 - May 18 to June 8 1944 - May 15 to June 1	73.5 - 81.7°F 78 - 84F
Jester (1962)	Conchas L., New Mexico	early May to mid-June peak in mid-May	65 - 75°F (18.3 - 23.9°C) 70°F (21.1°C) at peak
Jester and Jenkins (1972)	Elephant Butte L., New Mexico	May 7 to late June peak from May 15 to May 22	64 - 75°F (17.8 - 23.9°C)
Warner (1940)	Buckeye L., Ohio	Usually begins in early May	60°F when spawning starts
Bodola (1966)	L. Erie	Early June through early July Peak in second quarter of June	63 - 73°F (17.2 - 22.8°C)

observed only a low incidence of resorption of mature eggs in gizzard shad in the fall in Elephant Butte Lake.

Water temperature is an important factor in the initiation and continuation of spawning of gizzard shad (Bodola 1966). Gizzard shad spawning generally occurs between temperatures of 60 and 75°F (see Table 6). Peak spawning occurred in Conchas and Elephant Butte lakes at 70 and 66 - 68°F, respectively (Jester 1962, Jester and Jensen 1972). In Lake Erie, gizzard shad were common at the Fishery Bay spawning site at about 67°F and most common at about 70°F (Bodola 1966). Bodola (1966) found that the number of gizzard shad caught at the Fishery Bay spawning site dropped when water temperatures decreased slightly to 65 and 65.5°F. Miller (1960) indicated that gizzard shad generally spawn on a rising temperature but were observed spawning on a falling temperature on one occasion in Buckeye Lake, Ohio. Miller (1960) noted that water temperature during development of the eggs is probably more important in determining the time of peak spawning than is the water temperature immediately preceding the spawning period.

Spawning sites - Langlois (1954) observed gizzard shad spawning along the shore at depths of 6 to 12 inches (15 - 30 cm) in North Reservoir, Ohio. In Sandusky Bay, Ohio, shad were observed spawning along a stony shore in the shade of an overhanging tree (Bodola 1966). Bodola (1966) found gizzard shad spawning in Lake Erie over a bar about 200 feet long covered by 2 to 4 feet of water and having a bottom of sand, gravel and boulders.

Cladophora, *Myriophyllum*, and *Butomus umbellatus* were abundant during the spawning season (Bodola 1966). In Lake Erie, spawning was limited in the open lake (Bodola 1966). In Conchas Lake, New Mexico, the largest concentrations of spawning gizzard shad occurred on shallow silt beds, 1 to 6 feet (0.3 - 1.8 m) in depth, with most fish at depths less than 3 feet (Jester 1962). Gizzard shad in Elephant Butte Lake, New Mexico, spawn in depths ranging from a few inches to 40 and 50 feet (12 and 15 m) (Jester and Jensen 1972). Jester and Jensen (1972) observed the greatest concentrations of spawning shad in shallow coves in water depths of 1 to 5 feet (0.3 - 1.6 m). Many of these shad were observed spawning along the shore in 6 to 12 inches (15.2 - 30.5 cm) of water. Jester and Jensen (1972) also found spawning shad concentrated in unoccupied, covered boat docks in water about 50 feet deep.

Spawning behaviour - Direct observation in Ohio waters suggests that gizzard shad spawning occurs during the daytime (Scott and Crossman 1973), but Bodola (1966) found that spawning in Lake Erie was most active in the evening and at night.

Spawning male and female gizzard shad swim near the surface and begin to roll and tumble about each other in a mass, ejecting eggs and sperm (Miller 1960). The adhesive eggs sink or drift with the current, attaching to any object contacted, usually aquatic vegetation (Miller 1960). Langlois (1954) observed that when oviposition occurred a female was flanked on each side by a male. Jester and Jensen (1972) described the following behaviour

pattern of spawning gizzard shad in Elephant Butte Lake. One fish (assumed to be a female) was followed by 1 to 8 other fish, probably males. The males would periodically bump the female with their snouts. All fish swam on their sides. Occasionally, the group would begin to roll and tumble as described by Miller (1960).

Bodola (1966) found that females do not spawn their entire egg holdings on one visit to the spawning site.

Sexual maturity - Most gizzard shad in Lake Erie mature in age group II (Bodola 1966). Females older than age II were rarely immature (Bodola 1966). Bodola (1966) captured 3 mature I-group females (197 to 236 mm in standard length) and about 25 mature I-group males (190 to 230 mm in standard length) in Lake Erie. However, milt and spawn production by these precociously mature fish was scanty (Bodola 1966). Miller (1960) noted a report of a mature female 151 mm in total length and concluded that maturity may be attained at a much smaller size by gizzard shad than is commonly thought. In Elephant Butte Lake, male gizzard shad begin to mature in age group II and are all mature in age group IV and females mature in age groups III and IV (Jester and Jensen 1972). Jester and Jensen (1972) noted that many older females and a few older males were sexually inactive and had degenerated gonads.

Sex ratio - Table 7 shows the monthly sex ratios for gizzard shad from Lake Erie (Bodola 1966) and Elephant Butte Lake (Jester and Jensen 1972). The proportions of males in the populations,

Table 7. Monthly sex ratios for gizzard shad from Lake Erie, 1952 - 55 (Bodola 1966) and Elephant Butte Lake, 1970 (Jester and Jensen 1972).

	Jan.	Feb.	Mar.	April.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
Lake Erie													
Males	21	150	9	328	150	1004	299	237	534	451	901	259	4343
Females	39	123	14	361	208	849	510	229	678	458	969	340	4778
Percentage Males	35.0	54.9	39.1	47.6	41.9	54.2	37.0	50.9	44.1	49.6	48.2	43.2	47.6
Elephant Butte L.													
Males	4	29	25	129	552	370	178	78	110	136	35	66	1712
Females	13	38	21	64	167	121	137	119	121	138	38	96	1073
Percentage Males	23.5	43.3	54.3	66.8	76.8	75.4	56.5	39.6	47.6	49.6	48.0	40.7	61.5

averaged over the entire year, were 47.6% for Lake Erie and 61.5% for Elephant Butte Lake. Jester and Jensen (1972) suggested that the apparent preponderance of males in the April, May and June samples from Elephant Butte Lake probably resulted from their hyperactivity during the spawning season.

Bodola (1966) found that the proportion of males in the population in Lake Erie declined with age, from 45.6 - 49.7% in age groups 0-III to 38.6% in age groups IV-VI combined. Jester and Jensen (1972) reported a progressive decline in the proportion of males in Elephant Butte Lake as size increased. These observations suggest a shorter life expectancy for males, possibly due to their excessive activity during the spawning season which could result in a general decline in condition and in spawning mortalities (Jester and Jensen 1972).

Fecundity - Fecundities reported for gizzard shad by Bodola (1966) and Jester and Jensen (1972) are summarized in Table 8. Bodola (1966) found that egg production was low among precocious I-group fish, peaked at an average of 378,990 eggs per female among II-group fish and declined slowly among successively older females. Bodola (1966) noted that shad weighing 500 to 600 gm appeared to produce the most eggs. Jester and Jensen (1972) found that fecundity generally decreased with increases in size and age of gizzard shad in Elephant Butte Lake after peaking among females 180-189 mm in total length). The fecundity of gizzard shad in Elephant Butte Lake is much lower than that of Lake Erie shad, probably due to crowding in the former lake. Anderson (1973) noted an inverse

Table 8. Fecundity of gizzard shad.

Author and Location	Age	No. of fish	Length (mm)	Number of eggs per female	
				Range	Mean
Bodola (1966), Lake Erie	I	2	225 - 236 (SL[1])	22,400 - 96,560	59,480
	II	5	282 - 305	211,380 -543,910	378,990
	III	3	322 - 343	260,510 -406,170	344,780
	IV	2	348 - 363	267,220 -350,280	308,750
	VI	1	355	-	215,330
Jester and Jensen (1972) Elephant Butte Lake	III	26	172 - 208 (TL[2])	28,545 - 70,874	40,500
	IV	3	205 - 210	27,815 - 31,396	29,884
	VI	1	270	-	58,467

[1]SL = standard length

[2]TL = Total length

stock-recruitment relationship in gizzard shad. He suggested that low recruitment at high adult densities of shad may be related to poor maturation of eggs.

Early development and growth - On extrusion, gizzard shad eggs are about 0.75 mm in diameter (Miller 1960). Miller (1960) reported hatching times of 95 hours at 62°F (16.7°C) and about 36 hours at 80°F (26.7°C). Bodola (1966) found that hatching time varied from about 36 hours to 1 week, depending on water temperature.

Newly hatched gizzard shad larvae average 3.25 mm in total length and 0.2 mm in body depth (Miller 1960). Most of the yolk sac is absorbed in 1-day-old larvae which average about 5.5 mm in length (Miller 1960). Three-day-old larvae average 6.5 mm in length and have a complete alimentary canal and only a vestige of the yolk sac (Miller 1960). Gizzard shad reared by Bodola (1966) were 5.2 mm long in 4 days, began to feed during their fifth day and attained lengths of just over 6 mm by their tenth day. During the first couple of days after hatching, the behavior of shad larvae is characterized by alternate sinking and rising movements (Bodola 1966). On their fourth day, the shad begin to swim horizontally (Bodola 1966).

The growth of young-of-the-year gizzard shad in Lake Erie and Foots Pond, Indiana, is shown in Table 9. Miller (1960) reported average total lengths ranging from 4 to 5 inches for gizzard shad at the end of their first summer. The average

Table 9. Growth of young-of-the-year gizzard shad in Lake Erie and Foots Pond, Indiana.

Date	Average standard length (mm)	
	Foots Pond[1]	Lake Erie[2]
May 30	-	5
June 26	31.4	-
June 30	-	22
July 10	57.0	-
July 30	-	50
Aug. 20	66.6	-
Aug. 30	-	114
Sept. 30	-	155
Nov. 13	72.4	-
Dec. 30	-	165

[1] from Lagler and Applegate (1942)

[2] from Bodola (1966)

total lengths and length increments of gizzard shad at the time of annulus formation are shown in Table 10. Table 11 shows the average weights of gizzard shad at the time of annulus formation in Lake Erie and Elephant Butte Lake. Table 12 shows the number of years required in different localities for gizzard shad to attain a weight of 100 gm. The above tables indicate greatly varying growth rates for gizzard shad in differend localities. Except for during their first year, growth of gizzard shad in Crab Orchard Lake, Illinois, was slowest for all waters reported (Lewis 1953). Growth was fastest in Lake Erie (Bodola 1966), Lake Newman (Berry 1955) and Beaver Dam Lake (Lagler and Van Meter 1951). Average weights of gizzard shad in Elephant Butte Lake were much less than those of shad in Lake Erie (Table 11), probably due to intense intraspecific competition in the former lake (Jester and Jensen 1972).

Growth of gizzard shad is most rapid in the first year of life and shows a general decline in older age groups (Table 10). Lagler and Van Meter (1951) and Jester and Jensen (1972) found no evidence of significant sexual dimorphism of growth rates. However, Bodola (1966) found that after June of their second year of life female gizzard shad were consistently longer and heavier than males of the same age in Lake Erie. Lagler and Applegate (1942) reported a similar sexual dimorphism in the growth rate of shad in Grassy Pond, Indiana. Bodola (1966) found that most of the annual growth of shad in Lake Erie occurred between June and September. Gizzard shad show an exponential length-weight relationship (Figure 3).

Table 10. Grand mean lengths and increments of gizzard shad at time of annulus formation. Upper line is lengths and lower line is increments for each water. Shown in mm. Lengths are total lengths. (From Jester and Jensen 1972)

Locality (Author and date)	Grand Mean Lengths and Increments at Formation of Annulus										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Elephant Butte Lake, N.M.	94.4	150.5	183.3	218.6	253.9	273.0	291.0	323.8	-	-	-
(Jester and Jensen, new data)	94.4	56.1	32.8	35.3	35.3	19.0	18.0	32.8	-	-	-
Elephant Butte Lake, N.M.	85.9	127.9	156.0	184.8	213.7	233.5	238.4	259.5	-	-	-
(Patterson, 1968)	85.9	42.0	30.2	24.5	23.0	17.7	14.0	9.5	-	-	-
Conchas Lake, N.M.	75.8	153.8	225.0	284.3	320.0	342.5	360.3	370.8	378.5	386.5	411.5
(Jester, 1962)	75.8	78.0	71.2	59.3	35.7	22.5	17.8	10.5	7.7	8.0	25.0
Grand Lake, Okla.	100.0	202.5	260.0	317.5	350.0	382.5	395.0	-	-	-	-
(Jenkins, 1953a)	100.0	102.5	57.5	57.5	32.5	32.5	12.5	-	-	-	-
Tenkiller Reservoir, Okla.	140.0	237.5	350.0	385.0	422.5	422.5	-	-	-	-	-
(Hall and Jenkins, 1953)	140.0	97.5	112.5	35.0	37.5	0	-	-	-	-	-
Fort Gibson Reservoir, Okla.	142.5	257.5	325.0	-	-	-	-	-	-	-	-
(Jenkins, 1953b)	142.5	115.0	67.5	-	-	-	-	-	-	-	-
Spike Lake, Okla.	160.0	225.0	305.0	-	-	-	-	-	-	-	-
(Hall, 1951)	160.0	65.0	80.0	-	-	-	-	-	-	-	-
Poteau River, Okla.	197.5	227.5	310.0	330.0	357.5	-	-	-	-	-	-
(Hall, 1951)	197.5	30.0	82.5	20.0	27.5	-	-	-	-	-	-
Lake Erie	258.7	365.8	402.6	429.3	467.4	428.4	-	-	-	-	-
(Bodola, 1966)	258.7	107.1	36.8	26.7	38.1	-39.0	-	-	-	-	-
Foots Pond, Ind.	190.0	247.5	265.0	282.5	347.5	-	-	-	-	-	-
(Lagler and Applegate, 1942)	190.0	57.5	17.5	17.5	65.0	-	-	-	-	-	-
Grassy Pond, Ind.	192.5	227.5	257.5	282.5	295.0	-	-	-	-	-	-
(Lagler and Applegate, 1942)	192.5	35.0	30.0	25.0	12.5	-	-	-	-	-	-
Crab Orchard Lake, Ill.	100.8	136.1	167.1	170.1	162.5	-	-	-	-	-	-
(Lewis, 1953)	100.8	35.3	31.0	3.0	-7.6	-	-	-	-	-	-
Beaver Dam Lake, Ill.	240.0	277.5	330.0	375.0	-	-	-	-	-	-	-
(Lagler and Van Meter, 1951)	240.0	37.5	52.5	45.0	-	-	-	-	-	-	-
Lake Wappapello, Mo.	102.5	170.0	207.5	230.0	245.0	257.5	272.5	292.5	300.0	292.5	-
(Patriarche, 1953)	102.5	67.5	37.5	22.5	15.0	12.5	15.0	20.0	7.5	-7.5	-
Herrington Lake, Ky.	109.5	196.0	259.0	311.0	334.3	-	-	-	-	-	-
(Turner, 1953)	109.5	86.5	63.0	53.0	23.3	-	-	-	-	-	-
Lake Newnan, Fla.	253.6	316.7	338.2	-	-	-	-	-	-	-	-
(Berry, 1955)	253.6	62.0	22.6	-	-	-	-	-	-	-	-

Table 11. Weight (gm) of gizzard shad at time of annulus formation[1] in Lake Erie and Elephant Butte Lake.

Locality		I	II	III	IV	V	VI	VII	VIII
Elephant Butte Lake									
Patterson (1968)		4.4	16.2	30.9	53.6	85.9	114.6	122.7	161.7
Jester and Jensen (1972)		7.5	30.2	54.6	92.6	145.1	180.4	218.6	301.2
Lake Erie									
Bodola (1966)	Male	158	396	592	691	-	729*		
	Female	188	503	778	926	1082*	1114*		

*Asterisk indicates an average based on fewer than five fish

[1]Weight at time of annulus formation of shad in Lake Erie was approximated by listing the average weight of fish in each age group in June.

Table 12. Number of years required in different localities for gizzard shad to attain a weight of 100 gm (3.5 ozs.)

Author	Locality	Age at which 100 gm is attained
Lagler and Van Meter (1951)	Beaver Dam L., Ill.	<1 year
Berry (1955)	L. Newman, Fla.	<1 year
Bodola (1966)	L. Erie	<1 year
Lagler and Applegate (1942)	Foots Pond, Ind.	1 year
Turner (1953)	Herrington L., Ky.	2 years
Jester (1962)	Conchas L. N. Mexico	3 years
Patterson (1968)	Elephant Butte Lake, N. Mexico	5 years
Jester and Jensen (1972)	Elephant Butte Lake	4 years

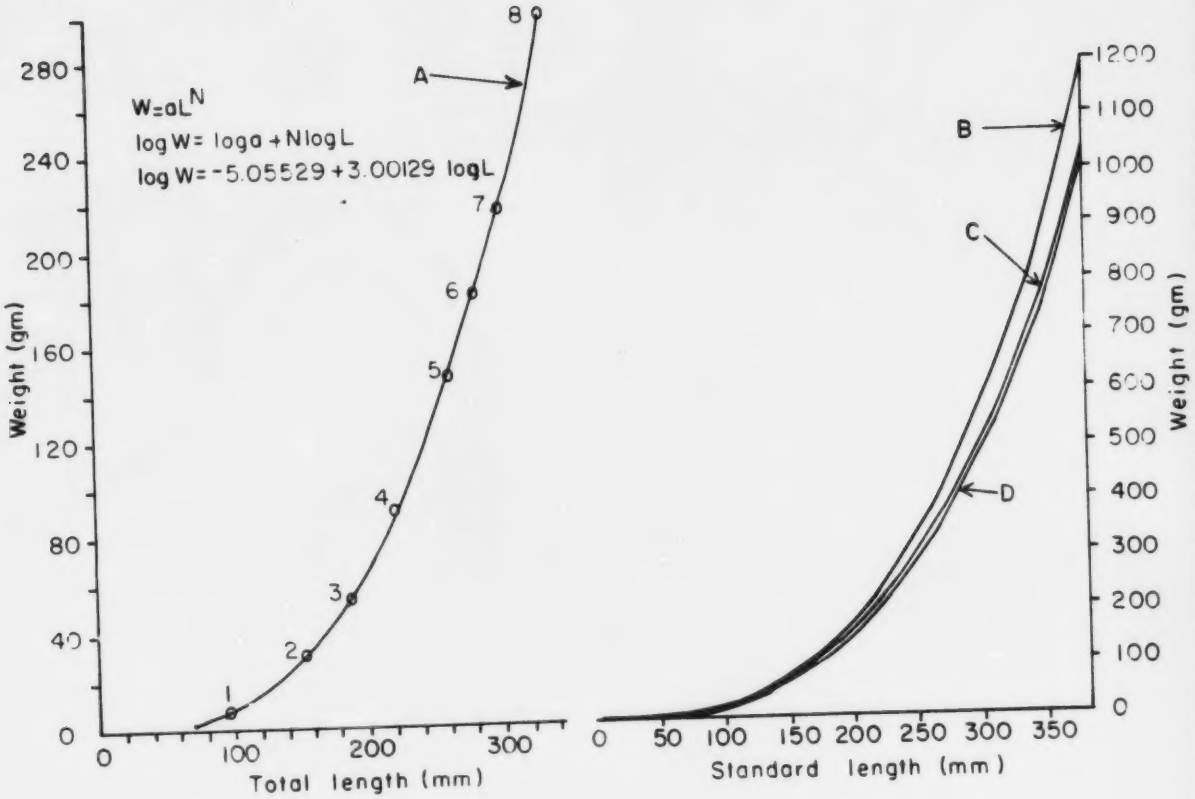

Figure 3. Length-weight curves for gizzard shad from Elephant Butte Lake (A), Lake Erie (B), Missouri (C), and Illinois (D) (from Bodola (1966) and Jester and Jensen (1972)).

The largest reported gizzard shad had a length of 520 mm (20.5 inches) and weighed 1559 gm (3 lb 7 oz) (Trautman 1957). Miller (1960) indicated that gizzard shad do not commonly grow longer than 254 - 356 mm (10 to 14 inches). The largest specimen caught by Jester and Jensen (1972) in Elephant Butte Lake was 338 mm (13.3 inches) long and weighed 354 gm (12.5 oz).

In Lake Newman, Florida, where gizzard shad growth was very rapid, only about 5% of the shad population approached their third year of life and no shad older than 4 years were found (Berry 1955). The oldest shad collected by Bodola (1966) in Lake Erie were 3 fish in age group VI. Jester and Jensen (1972) caught a few shad in age group VIII in Elephant Butte Lake. Jester (1962) caught gizzard shad as old as age group XI in Conchas Lake, New Mexico. Patriarche (1953) found 10-year-old gizzard shad in Lake Wappapello but stated that in other Missouri reservoirs the species lives no longer than 5 to 6 years.

Food habits - Gizzard shad begin to feed 4 to 5 days after hatching (Bodola 1966). Bodola (1966) indicated that the earliest food of shad is probably protozoans and unicellular algae and that at a length of about 20 mm shad feed on smaller zooplankton but take practically no phytoplankton. Miller (1960) reported that gizzard shad eat mainly protozoans and entomostracans during their first few weeks of life. Warner (1940) found that the stomach contents of gizzard shad up to about 22 mm long consisted almost entirely of cladocerans (*Bosmina*), copepods and a few ostracods. Cramer and Marzolf (1970) reported that gizzard shad

less than 20 mm long utilized crustacean zooplankton almost exclusively, most frequently ingesting *Cyclops*, *Bosmina*, and *Daphnia*. They suggested that young gizzard shad select against phytoplankton food resources and select from among the types of zooplankton organisms available to them as food. They indicated that organism size was a highly significant factor influencing this selection and suggested that instead of randomly filter feeding, small shad probably pick larger zooplankters individually by choice. Kutkuhn (1957) made a similar suggestion, noting that very small shad in North Twin Lake, Iowa, utilized the largest zooplankton (*Daphnia longispina* and *Asplanchna priodonta*, for example). Cramer and Marzolf (1970) found that selective predation by young shad apparently had a noticeable impact on zooplankton populations in Tuttle Creek Reservoir, Kansas. After small shad appeared in the reservoir, they observed a decrease in zooplankton density, especially in the species selected for by young shad, and a change in the speices composition of the zooplankton, with the percentage of species selected for by shad decreasing in the population.

Many authors describe a change in diet from predominantly zooplankton to mainly phytoplankton in shad between 22 and 32 mm in length. Miller (1960) noted that gizzard shad 26 mm long contained largely algal plankton (diatoms, desmids and colonial forms) and shelled and flagellated protozoans (*Euglena*). Cramer and Marzolf (1970) found that shad longer than 20 mm ingested increasing amounts of phytoplankton. They reported that phytoplankton was the major component of the shad's diet by the time they had grown to lengths of 28 to 30 mm and that

no recognizable zooplankton was found in shad over 45 mm long. Of the zooplankton eaten by shad over 35 mm long, small forms such as the rotifer *Keratella* were most common (Cramer and Marzolf 1970). Bodola (1966) noted that gizzard shad begin to feed increasingly on phytoplankton by the time they reach lengths of about 30 mm. Cramer and Marzolf (1970) related this change in diet to the development of the gizzard and of the straining apparatus of the gills and to increases in the length and number of flexures of the gut. They noted indications of a trend toward smaller spaces between the gill rakers as shad grow, allowing the retention of smaller food items.

Scott and Crossman (1973) stated that "fully developed gizzard shad are herbivorous, feeding on the bottom on microscopic plants or phytoplankton and algae." Tiffany (1921) indicated that gizzard shad feed by swimming through the water in an apparently aimless manner, filtering food organisms from the water with their many fine gill rakers. He reported a diet of 70-90% microalgae, 0-15% microanimals, 0-5% filamentous algae, 5-20% plant debris and usually 10-20% mud for young gizzard shad in Ohio lakes. Tiffany (1921) noted a similar diet for older shad 200 mm long. Tiffany's studies indicated that gizzard shad are almost entirely herbivorous. However, Velasquez (1939) found that algae often pass undigested through the digestive tracts of gizzard shad. Jude (1973) suggested that shad therefore probably derive little energy from ingested algae.

Results of other studies indicate a more variable diet for adult gizzard shad. Ewers and Boesel (1936) found that the

gut contents of shad 22 to 31 mm long in Buckeye Lake, Ontario, were 14% Cladocera and 86% algae and debris. Berry (1955) reported that the gut contents of shad in Lake Newman, Florida, were 7.9% algae, 1.0% plant remains, 9.0% Crustacea, 0.1% Hydracarina, 4.0% sand and 78% debris. Rice (1942) reported a diet of 75% crustaceans, 10% insect larvae and 15% diatoms for gizzard shad. Ried (1949) found the gut contents of gizzard shad to be almost entirely ostracods, copepods and cladocerans, with phytoplankton, mainly Chlorophyta, Cyanophyta and Crysophyta, was usually the major contributor to shad diets in North Twin Lake, Iowa, he also noted that zooplankton (mainly crustaceans) averaged about one-fourth of the total volume of ingested plankton. Jester and Jensen (1972) found that unidentified organic residue, Chlorophyta, *Bosmina*, Chrysophyta and *Diaptomus* were the most numerous items in the digestive tracts of gizzard shad in Elephant Butte Lake. They found that phytoplankton comprised 36.8% of the total number of food items counted, zooplankton made up 31.2%, unidentified organic residue 28.4% and higher plant material 3.6%. Phytoplankton was more abundant than zooplankton in terms of numerical abundance, but zooplankton comprised the greater biomass (Jester and Jensen 1972). Jester and Jensen (1972) concluded that the food ingested by gizzard shad is primarily incidental to its activities with the habitat. Bodola (1966) related variation in the food items of gizzard shad to local and seasonal variation in the abundance of various food items in the shad's habitat and to unselective filter feeding by the shad. He noted that gizzard shad captured in open waters contained

mostly free-floating phytoplankton, that those caught among littoral vegetation had ingested cladocerans, copepods, rotifers and small aquatic insect larvae, and that those collected in very turbid water contained much mud in their digestive tracts. However, Kutkuhn (1957) presented evidence that gizzard shad do not filter feed randomly but show a high degree of selectivity for certain organisms, especially certain blue-green algae.

In addition to filtering suspended material, feeding behaviour of gizzard shad must also include some type of bottom-probing activity. Bodola (1966) found sand particles too large to be in suspension in the gizzards of shad in Lake Erie. He suggested that this sand may have been ingested accidentally along with food or to use as an aid in grinding by the gizzard. Freeman and Huish (1953) reported that chironomid larvae and molluscs were the main portion of the identifiable food of shad in two Florida lakes. Minckley (1963) listed chironomids, oligochaetes, diatoms and *Spirogyra* as the principle foods of gizzard shad in a Kentucky stream. Jude (1973) found that sphaeriids, algae and unidentified material formed the bulk of the stomach contents of larger gizzard shad in Pool 19 of the Mississippi River.

Dendy (1946b) found that gizzard shad are occasionally cannibalistic. Jester (1962) reported that several large shad (380-435 mm long) have been caught on hooks baited with small fathead minnows.

Bodola (1966) observed that gizzard shad in Lake Erie

appeared to eat little in winter and early spring. Jude (1973) found that intensive feeding by shad in Pool 19 began in April or early May and ended by early September. In Pool 19, maximum or near maximum meals were eaten by shad soon after feeding began, generally in May (Jude 1973). Most feeding apparently occurred during daylight hours in Pool 19 (Jude 1973).

Parasites - Miller (1960) indicated that gizzard shad are generally free from parasites. He noted, however, that young shad in Buckeye Lake, Ohio, may often be heavily infested with a microsporidian which forms large white cysts in the body cavity. Bangham and Hunter (1939) found a single nematode *(Agamonema sp.)* in one of five gizzard shad examined from Lake Erie. Van Cleve found two species of Acanthocephala in 300 gizzard shad and Essex and Hunter reported no parasites in over 100 shad from Mississippi (Bangham and Hunter 1939). Hanek and Fernando (1971) found five specimens of the monogenoidean parasite *Pseudomazocraeoides ontariensis* in three gizzard shad from the Bay of Quinte. Jester and Jensen (1972) found one specimen of the ectoparasite *Argulus* and of the acanthocephalan *Gracilicentis* in gizzard shad from Elephant Butte Lake. Smith (1949) found the copepod parasite *Ergasilus lanceolatus* in gizzard shad in the Cumberland River, Kentucky. Van Cleave and Mueller (1934) reported the cestode *Glaridacris confusus* in the intestine of shad in Oneida Lake, New York. Hoffman (1967) listed Protozoa (1), Trematoda (8), Cestoda (2), Acanthocephala (3) and Crustacea (3) from gizzard shad in North American fresh waters.

Predators - Table 13 lists the fish species known to prey upon gizzard shad. Dendy (1946b) noted that gizzard shad was the most important food of game fishes in Norris Reservoir. Schneidermeyer and Lewis (1956) found that in Crab Orchard Lake, Illinois, gizzard shad occurred in 85 of 107 largemouth bass stomachs containing food. Bonn (1952) found that gizzard shad was the only vertebrate eaten by young white bass in Lake Texoma. Kutkuhn (1958) reported that gizzard shad was the most important part of the diet of northern pike in North Twin Lake. In five Oklahoma reservoirs, gizzard shad comprised 76.1, 84 and 59 percent of the total volume of food of total volume of food of flathead catfish, freshwater drum and longnose gar, respectively (Summerfelt 1968). Ranthum (1969) indicated that gizzard shad was the chief component of the diet of many fishes, especially sauger and white bass, in the Mississippi River. In Elephant Butte Lake, gizzard shad totalled 93.6, 91.7, 77.5 and 68.8 percent of the number of items found in stomachs of walleye, channel catfish, white bass and largemouth bass, respectively (Jester and Jensen 1972).

Gizzard shad are apparently subject to heavy predation only when small. Patterson (1968) found that gizzard shad in Elephant Butte Lake are subject to heavy and moderate predation only up to lengths of 130 and 200 mm, respectively. Ranthum (1969) indicated that shad are essentially invulnerable to all fish predators after attaining lengths of 152 mm or more. In Lake Erie, shad in age groups I and older are usually too large to be eaten by most predatory fish (Bodola 1966). Miller

Table 13. Fish species preying on gizzard shad.

Author	Location	Species Preying on Gizzard Shad
Wickliff and Trautman (1931)	Ohio ponds and lakes	white bass *(Morone chrysops)* largemouth bass *(Micropterus salmoides)* and white crappie *(Pomoxis annularis)*
Lagler, Obrecht and Harry (1943); Lagler and Ricker (1943)	Foots Pond, Indiana	gars *(Lepisosteus platostomus, L. productus, L. osseus)*, white bass, largemouth bass, white crappie and black crappie *(Pomoxis nigromaculatus)*
Bonham (1941)	Texas	*L. productus, L. osseus*
Forbes (1888)	Illinois	skipjack *(Alosa chrysochloris)*, northern pike *(Esox lucius)* yellow bullhead *(Ictalurus natalis)* and white crappie
Forbes (1903)	Illinois River	walleye *(Stizostedion vitreum)*, sauger *(S. canadense)*, and yellow bass *(Morone mississippiensis)*
Dendy (1946b)	Norris Reservoir Tennessee	channel catfish *(Ictalurus punctatus)*, largemouth bass, smallmouth bass *(Micropterus dolomieui)* spotted bass *(M. punctulatus)*, black crappie, walleye, sauger, freshwater drum *(Aplodinotus grunniens)*.
Eschmeyer (1944)	Clinch River Tennessee	white bass, largemouth bass
Summerfelt (1968)	Oklahoma reservoirs	flathead catfish *(Pylodictus olivarus* ,freshwater drum, and longnose gar *(L. osseus)*
Kutkuhn (1958)	North Twin Lake, Iowa	yellow bass, yellow perch, walleye, black crappie, largemouth bass, black bullhead
Jester (1962)	Conchas Lake, New Mexico	largemouth bass, white crappie, black crappie, channel catfish, walleye, black bullhead, yellow bullhead, blue catfish and a single rainbow trout *(Salmo gairdneri)*
Jester and Jensen (1972)	Elephant Butte Lake, New Mexico	northern pike, walleye, channel catfish, white bass, largemouth bass
Lagler and Hubbs (1940)		bowfin *(Amia calva)*
Galligan (1951)	Cayuga Lake, New York	lake trout *(Salvelinus namaycush)* (a single gizzard shad was found in one of 312 stomachs examined)

(1960) noted that only young-of-the-year gizzard shad about 2 to 5 inches long are of major value as forage. Stroud (1949) found that walleye fed heavily on gizzard shad up to 75 mm (3 inches) long, many contained shad up to 125 mm (5 inches) long, and a few contained shad up to 335 mm (13.2 inches) long. Forbes (1903) reported that walleye, sauger and yellow bass in the Illinois River preyed upon gizzard shad between 75 and 100 mm (3 and 4 inches) long. Jester (1962) found gizzard shad up to 200 mm (8 inches) long in walleye in Conchas Lake. Game fishes in Elephant Butte Lake commonly take shad up to 200 mm long (Jester and Jensen 1972). Largemouth bass in Crab Orchard Lake contained shad up to 250 mm (10 inches) long (Dubets, 1954). Parsons (1971) indicated that gizzard shad constituted a relatively unimportant food of walleyes in Lake Erie in 1960. He noted that the 1959 year class of shad grew so fast in Lake Erie that most exceeded the maximum lengths of forage fish preferred by walleyes by August. Jenkens (1959) noted that fast growth rendered gizzard shad unavailable as forage after their first summer of life in a small Oklahoma lake. Scott and Crossman (1973) stated that only large predators such as northern pike, muskellunge, channel catfish and large walleyes could eat adult gizzard shad and that there are few records of such predation in Ontario waters.

Mauck and Coble (1971) found that small gizzard shad (about 30 to 192 mm long) were the most vulnerable to northern

pike predation of the fishes that they studied. Kutkuhn (1957) noted evidence that gizzard shad might be a select prey species in North Twin Lake. Kutkuhn (1957) and Ranthum (1969) suggested that gizzard shad may be an important buffer species, reducing predation on other fishes.

Abundance - Jester and Jensen (1972) noted that, because of a high reproductive potential and rapid growth rate, gizzard shad tend to overpopulate many waters to the detriment of other fish populations. Bodola (1966) noted that the stocks of gizzard shad in Lake Erie have increased enormously since 1950, creating esthetic and public-health problems due to their frequent mass mortalities, plugging water intakes and plaguing commercial fishermen. In Clearwater Lake, Missouri, the abundance of gizzard shad increased phenomenally after impoundment, its percentage composition rising from 2.0 in 1949 to 57.8 in 1950 (Miller 1960). Gizzard shad were first netted in Black Hawk Lake, Iowa, in 1945 and had reached nuisance levels by 1947 (Miller 1960). About 7,360 young gizzard shad per acre were removed from the lake in the fall of 1951 despite prior stocking of predators to keep the shad in check (Miller 1960). In Lake Apopka, Florida, shad increased to the point where they constituted over 80 percent of the total fish population (Heinen 1958). Miller (1960) noted similar overpopulations of gizzard shad in other Florida Lakes. Lagler and Van Meter (1951) found that gizzard shad and bluegills usurped most of the fish producing capacity of Beaver Dam Lake, Illinois, and that largemouth bass were unable to significantly regulate the populations of these two species. Miller (1960)

concluded that gizzard shad populations are likely to mushroom in shallow, warm-water lakes with a mud bottom, high turbidity and high fertility, even if numbers of predatory fishes are present, especially if the shad are not native to such waters.

Competition with other fishes - Many workers have found indications of an adverse effect of gizzard shad upon other fishes. Bennett (1943) found that large shad populations were always associated with small numbers of bass in artificial warm-water lakes in Illinois. He noted that, in 5 of the 10 lakes in which shad occurred, they constituted 48 to 65 percent of the total fish populations (by weight) and the game and pan fishes were small and stunted. Swingle (1949) showed that the presence of shad reduced the size of adult bluegills in Alabama ponds where the two species competed for food. Thompson (1941) indicated that large populations of gizzard shad may be partially responsible for high turbidity in some waters, thus leading to a decrease in the productivity of game fishes. Game fishes were suppressed by the explosion of shad in Black Hawk Lake, Iowa (Madden 1951). Miller (1960) noted that the increase of shad in this lake also coincided with a decline in bottom organisms. The increase of shad in Lake Apopka coincided with a marked decrease of sport fishing and a change in the lake from clear water and large quantities of submerged vegetation to turbid water and sparse submerged plants (Miller 1960). Jenkens (1957) found that sunfishes had a plumper condition, faster growth, and greater average length in a small

Oklahoma lake without shad than in one with shad; this indicated direct competition between centrachids and gizzard shad in small lake populations. Kutkuhn (1957) stated that recently hatched gizzard shad and various game and pan fishes concomitantly consumed certain crustaceans almost exclusively during spring and early summer in North Twin Lake, Iowa, indicating potential competition between shad and these species for food. He also noted comparatively poor survival of young yellow bass in years when gizzard shad were abundant. Shad removal in Kentucky resulted in improved angler success and increased bass spawning and survival (Smith 1959). Cramer and Marzolf (1970) suggested the possible occurrence of competition between young game fish and young gizzard shad, noting that the young of most game fishes (for example, largemouth bass, walleye and white crappie) utilized crustacean zooplankton for at least a short time after hatching in Tuttle Creek Reservoir. This suggestion is supported by an increase in fishing success and the numbers of some game fishes in southern reservoirs after selective poisoning of gizzard shad (Zellar and Wyatt 1967).

The effects of selective predation by gizzard shad on the zooplankton population in Tuttle Creek Reservoir have been discussed above. Velasquez (1939) considered herbivorous fish such as the gizzard shad to be a possible source of selective increases or decreases of certain algae. He suggested that they may tend to eliminate phytoplankters most desirable as fish food and favor increases of less desirable ones. The occurrence of changes in plankton populations as a result of feeding by gizzard

shad indicate rates of consumption great enough to exert a detrimental effect upon other fish species.

Forage value - Miller (1960) listed the important qualifications of gizzard shad as forage. He noted its direct utilization of phytoplankton, high reproductive capacity and abundance, general freedom from parasites, rapid growth rate and utilization as food by important game species. Hubbs and Eschmeyer (1938) also noted that the adults are too large to be readily eaten, assuring ample breeding stocks. Hubbs (1934) considered gizzard shad "the most efficient biologically of all the forage fishes" because it represented a short, efficient food chain link directly connecting phytoplankton with game fishes. Jude (1973) concluded that gizzard shad played a very important role as a forage fish in Pool 19 of the Mississippi River where they were responsible for the conversion of detritus and sphaeriids, a relatively unused faunal resource, into fish flesh. Wickliff (1933) held the gizzard shad in high esteem as a forage fish, stating that its presence or absence seemed to determine whether or not impounded waters in Ohio would be productive of several game fishes. Miller (1960) concluded that the gizzard shad is an ideal forage fish in fluctuating impoundments "where the water is deep and clear, the shoreline is abrupt, no littoral vegetation develops, there is a paucity of benthic flora and fauna but adequate plankton, and sufficient predatory species are present to crop the young-of-the-year".

However, under many conditions, gizzard shad may not be a suitable forage fish. Firstly, it is often not entirely, or even chiefly, herbivorous and thus does not represent the very

short, efficient food chain link described by Hubbs (1934). Instead, much of its diet consists of zooplankton and, on occasion, benthic animals, thus placing it in competition with the young of many game fishes for food. Secondly, because of its rapid growth to a size not eaten by predators and its high reproductive capacity, it tends to overpopulate many waters and suppress game fishes.

Summary

Gizzard shad frequent brackish waters with salinities from 2.0 to 33.7 parts per thousand and occur in a wide variety of freshwater habitats ranging from swamps and temporary flood-water pools to large rivers, reservoirs and lakes. They occupy chiefly the littoral and limnetic areas of lakes. Adults migrate into shallow water during the spawning season and may ascent small streams and ditches to spawn. Young gizzard shad live near shore in mid-summer, usually in shallow water. In Elephant Butte Lake, shad apparently move into deeper areas and cease activity almost entirely as the water temperature approaches 14°C.

Young-of-the-year gizzard shad occur in compact schools soon after hatching. Large schools of shad of all ages have been observed at Conchas Lake.

At acclimation temperatures of 25 and 30°C, the upper and lower lethal temperatures for gizzard shad are 34.3 and 10.8°C and 35.9 and 14.5°C, respectively. High winter mortalities of gizzard shad occur in New Mexico lakes below temperatures ranging

from 2.2 to 3.0°C. Winter mortalities of shad in Lake Erie have been associated with sudden rises in water temperature. Shad concentrate near warm inflowing streams and the outlets of industrial plants in winter in Lake Erie.

Gizzard shad spawning occurs between March and mid-August in southern U.S. waters. In Lake Erie and South Dakota, most spawning occurs in June and early July. Precociously mature I-group shad might spawn in late July or early August in Lake Erie. A second but less pronounced spawning period might occur in late summer in southern regions. Spawning generally occurs between water temperatures of 60 and 75°F. Peak spawning occurs at 66 to 70°F. Spawning occurs near the surface in water ranging from 6 inches to 50 feet in depth, but usually in depths less than 6 feet.

Most gizzard shad in Lake Erie mature in age group II but some precociously mature I-group shad have been collected. In Elephant Butte Lake, male and female shad mature in age groups II to IV and III and IV, respectively.

The average proportions of males reported for populations in Lake Erie and Elephant Butte Lake are 47.6% and 61.5%, respectively. The proportion of males declines as age and size increase, suggesting a shorter life expectancy for males than females.

In Lake Erie, fecundity peaks at an average of 378,990 eggs per female among II-group fish. Fish weighing 500 to 600 gm appear to produce the most eggs. Fecundity peaks among females

180 - 189 mm long in Elephant Butte Lake. Gizzard shad display an inverse stock-recruitment relationship.

Gizzard shad eggs are about 0.75 mm in diameter. Hatching time varies from about 36 hours (at 80°F) to a week, depending on water temperature. Newly hatched larvae average 3.25 mm in total length. Growth rate is most rapid during the first year of life. Growth rates vary greatly among shad in different localities. Gizzard shad show an exponential length-weight relationship. The largest reported gizzard shad was 20.5 inches (520 mm) long and weighed 3 lb 7 oz (1559 gm). Gizzard shad as old as age group XI have been captured but most shad live no longer than 5 to 6 years.

Gizzard shad begin to feed 4 to 5 days after hatching. The earliest food items of shad include protozoans, entomostracans and unicellular algae. Gizzard shad of lengths up to about 22 mm feed almost entirely on crustacean zooplankton. Young shad display selective predation, probably picking larger zooplankters individually by choice. Predation by young shad may have a noticeable impact on zooplankton populations. Many authors describe a change in diet from predominantly zooplankton to mainly phytoplankton in shad between 22 and 32 mm in length. Adult gizzard shad have been considered to be almost entirely herbivorous. However, algae often pass undigested through shad digestive tracts. Therefore, gizzard shad might derive little energy from ingested algae. Crustacean zooplankton and occasionally molluscs and chironomid larvae are major constituents of the diets of adult gizzard shad. Gizzard shad are occasionally cannibalistic.

Most feeding by gizzard shad occurs during daylight hours between spring and early fall.

Gizzard shad generally have few parasites. Gizzard shad are a major component of the diets of many game fishes in some waters. Shad are subject to heavy predation only when small. In some waters, gizzard shad may be an important buffer species, reducing predation on other fishes.

Because of their high reproductive potential and rapid growth rate, gizzard shad tend to overpopulate many waters to the detriment of other fish populations. Overpopulation by gizzard shad is most likely to occur in shallow, warm-water lakes with mud bottoms, high turbidity and high fertility, especially if the species is not native to such waters. Many workers have found indications of an adverse effect of gizzard shad upon other fishes. This effect might result from competition between young game fish and young gizzard shad for food.

The gizzard shad has been considered to be an ideal forage fish because of its high reproductive capacity, general freedom from parasites, rapid growth rate, utilization as food by game fishes and supposedly herbivorous diet. However, it is often not a suitable forage fish because it consumes large amounts of zooplankton and occasionally benthic animals and tends to overpopulate many waters, thereby suppressing game fish populations.

LIFE HISTORY OF THE PADDLEFISH

Introduction

The paddlefish, *Polyodon spathula* Walbaum, represents one of the more primitive groups of fishes, as evidenced by its chiefly cartilaginous skeleton. It is distinguished by an elongated, paddle-shaped snout.

The paddlefish is found in the larger streams of the Mississippi River drainage, ranging from the Missouri River, in eastern Montana, eastward to Pennsylvania and New York and southward to western North Carolina, Mississippi, Louisiana and Texas (Hubbs and Lagler 1964). Hubbs and Lagler (1964) noted early reports of paddlefish for Lake Erie, Spanish River on Georgian Bay, Lake Huron near Sarnia, Lake Winnebago or Green Bay (before 1700), Lake Helen on the Nipigon River and, doubtfully, Lake Ontario. Trautman (1957) indicated that a small paddlefish apparently existed in Lake Erie until at least 1903. Greene (1935) concluded that paddlefish probably invaded Lake Erie through canals but Trautman (1957) indicated that the species was probably present in the lake as a relect population before the building of canals. Hubbs and Lagler (1964) noted that paddlefish may now be extinct in the Great Lakes and are much depleted in the northern part of their Mississippi Valley range.

This paper reviews the relatively scanty information existing on the life history of the paddlefish.

The Life History of the Paddlefish

Habitat and movements - The paddlefish is essentially an inhabitant of the open waters of large silty rivers and of oxbow

and flood-plain lakes (Hubbs and Lagler 1964). Trautman (1957) indicated that paddlefish inhabit "the sluggish pools, back-waters, bayous and oxbows of large river, where the gradient is low". In South Dakota, paddlefish congregate in the Missouri River and its tributaries in deep holes with a fairly strong current, in reservoirs at river mouths and up streams that enter the reservoirs and in tailwaters immediately below power outlets (Fogle, year unknown). Cross (1967) indicated that lakes or large pools with silty bottoms are the primary feeding areas of paddlefish.

Trautman (1957) noted that paddlefish are apparently highly migratory. According to Trautman, paddlefish seem to rarely move upstream during floods, migrating instead when water levels are lower and currents weaker. Paddlefish apparently migrate mostly near the surface (Evermann 1902).

Purkett (1961, 1963) described the movements of paddlefish in the Osage River and the Lake of the Ozarks, Missouri. Paddlefish were present in the headwaters of the Lake of the Ozarks in late February. Extensive upstream migration to spawning sites in the Osage River occurred when the water warmed to near 50°F and water levels rose due to heavy rains. The fish moved downstream when water levels fell. Fish which had not yet spawned moved back upstream during the next rise in water level. Spent fish apparently returned to the Lake of the Ozarks immediately after spawning. Newly hatched fry were apparently swept to the headwaters of the lake within several days of hatching. Most fish were in the lake in the fall. Purkett's observations indicate that high water levels are required for upstream migrations of paddlefish, and contradict Trautman's statements on

paddlefish migrations.

Spawning season - Carlander (1969) noted that gravid female paddlefish have been collected in September and from January through June and that males with sperm have been found in all seasons. Carlander (1969) reported that paddlefish spawn from March to June. Paddlefish spawning occurred between mid and late April in the Osage River and its tributaries in 1958, 1960, and 1961 (Purkett 1961, 1963). In the Osage River, spawning occurred at water temperatures above 50°F and several days after water levels had risen 9 or more feet above normal (Purkett 1961, 1963). Purkett (1961) noted a possible second spawning period in early May in the Osage River after rains raised the water level 11 feet.

Purkett (1961) found no evidence of spawning upstream in the Osage River in 1959, possibly due to the infrequency of spring rises in water level that year. However, paddlefish spawning may have occurred further downstream. Houser and Bross (1959) found that paddlefish spawning occurred in 1950 and 1957, but not in the intervening years, in Fort Gibson Reservoir, Oklahoma.

Spawning sites - Stockard (1907) indicated that paddlefish spawn only in running water. Katz (1954) reported that paddlefish spawn in schools over sand and pebbles. Purkett (1961) found paddlefish spawning over a large gravel bar in the Osage River in rapidly flowing water. Most of the gravel in the bar ranged from 0.5 to 1.5 inches in diameter. Depth fluctuated considerably with water level. Turbidity was 180 ppm and water temperature 61°F during

the spawning period. Purkett (1961) found eggs or dead larvae on many other small-gravel bars in the river but never on bars composed of large rubble or boulders. He suggested that the swifter current over the large rubble might be a deterring factor. Meyer and Stevenson (1962) stated that paddlefish will not spawn naturally in reservoirs but Houser and Bross (1959) reported spawning occurred in Fort Gibson Reservoir in some years when spring currents were strong enough to be noticeable in the main part of the reservoir.

Spawning behaviour - Purkett (1961) observed paddlefish spawning in the late afternoon and evening. Most spawning activity occurred well below the surface although single fish occasionally approached the surface and agitated their caudal fin several times. Purkett (1961) concluded that this surfacing was the end of spawning "rushes" of the females. He suggested that these spawning rushes occurred from a considerable distance under the surface and that during these rushes eggs were released by a rapid agitation of the caudal fin of the female. Presumably, accompanying males then released milt.

Sexual maturity - The smallest mature males and females reported by Meyer (1960) weighed 2270 and 2950 gm, respectively. Meyer and Stevenson (1962) reported sexually inactive males and females weighing 3630 to 6810 gm and a sexually inactive female weighing 11350 gm. Adams (1942) stated that female

paddlefish mature sexually at an age of about 7 or 8 years. Katz (1954) indicated that males first mature at 998 mm or 7 years and females at 1067 mm or 9 to 10 years. Sprague (1961) reported that sperm or eggs begin developing at age V and take about 2 years to mature. Judging from the crowding of annuli, females spawn at intervals of 4 to 7 years (Carlander 1969). Houser and Bross (1959) also suggested that paddlefish have a periodicity in their sexual maturation and noted that no apparent paddlefish spawning occurred in Fort Gibson Reservoir in 1951, 1952 and 1958, despite evidently favorable conditions in these years. Purkett (1963) found that some paddlefish participated in spawning migrations in the Osage River in at least two consecutive years.

Fecundity - Meyer (1960) reported that two females 1374 mm long contained 137,247 and 141,531 eggs.

Early development and growth - The diameter of fertilized eggs averages 3.0 mm and ranges from 2.7 to 4.0 mm (Purkett 1961). Paddlefish eggs become adhesive immediately after fertilization, usually adhering singly to pebbles or rocks (Purkett 1961). Purkett (1961) found that the most favourable locations for hatching of paddlefish eggs were clean-swept gravel bars where aeration was good and eggs were not subject to siltation. Many eggs were, however, swept downstream and coated with debris before becoming attached to gravel. The viability of loose and free-floating eggs was much lower than that of eggs attached to gravel. Purkett (1961) found that many eggs incubating on gravel bars were subject to desiccation due to rapidly falling water levels

after spawning.

At water temperatures of 65 to 70°F, eggs hatched in 7 days or less in the Osage River (Purkett 1961). Hatching occurred much more quickly in isolated pools where the water temperature was much higher. Purkett (1961) noted that the firm attachment of eggs to gravel was important in facilitating the escape of fry from eggs.

Newly hatched fry vary from 8.0 to 9.5 mm in total length (Purkett 1961). A few minutes after hatching, the fry begin continuous erratic swimming from the bottom to the surface, resting only while gliding back to the bottom (Purkett 1961). Enough yolk is absorbed in 2 to 3 days to permit the fry to swim in a straight line. In the Osage River, this continuous swimming caused most fry to be swept downstream from the gravel bars to deep water before flood waters receded and desiccation occurred (Purkett 1961).

The sizes of paddlefish at various ages from different areas throughout its range are presented by Carlander (1969). Growth was much faster in Fort Gibson Reservoir than in any other body of water studied (Table 14). The rapid growth in this reservoir was associated with changes caused by impoundment (Linton 1961). Purkett (1961) found that female paddlefish averaged larger than males. However, Purkett (1961) attributed much of the greater weight of the females to the weight of the ovaries. Sprague (1959) found no sexual dimorphism in growth rates of paddlefish.

Table 14. Calculated total length (mm) of paddlefish at each annulus (from Carlander 1969).

Location	No.	Calculated total length (mm) at each annulus						
		1	2	3	4	5	6	7
Arkansas and Cimarron Rivers, Oklahoma	19	292	424	521	612	701	732	795
Fort Gibson Reservoir, Oklahoma	28	363	533	706	1006	1148	1257	1131
	16	206	432	-	-	-	-	-

Tables 15 and 16 display the length-weight relationship of paddlefish. Equations describing this relationship are shown in Table 17. Coefficients of condition reported for paddlefish are given in Table 18.

The largest reported paddlefish was 1524 mm long and weighed 83.5 kg (Trautman 1957). Paddlefish as old as 30 years have been collected (Purkett 1963).

Food habits - The feeding habits of paddlefish have been a matter of controversy. Forbes, cited by Eddy and Simer (1929), indicated that paddlefish feed entirely on plankton. Jordan and Evermann (1896), Imms (1904), and Stockard (1907) believed that they are partly bottom feeders. Forbes and Richardson (1908) found no evidence of mud or bottom fauna in paddlefish stomachs. Eddy and Simer (1929) concluded that paddlefish are mainly planktonivorous. The occasional occurrence of bottom organisms in their diets probably result from the stirring up of these organisms into the water column by river conditions.

Table 19 lists the stomach contents reported by Eddy and Simer (1929) for paddlefish in McIntyre Lake, Mississippi, and in the Illinois River. Copepods, cladocerans and *Corethra* larvae comprised the bulk of the stomach contents. Eddy and Simer (1929) noted that the gill rakers retained only the larger plankton species, resulting in a paucity of smaller cladocerans, rotifers, protozoans and algae in paddlefish diets. A collection of items from the gills of a paddlefish in March provided the only evidence observed by Eddy and Simer (1929)

Table 15. Standard length-weight relationship of paddlefish. Lengths are in mm and weights in gm (from Carlander 1969).

SL	No.	Weight	SL	No.	Weight
178-202	1	54	991-1015	4	5534
305-329	1	100	1016-1040	1	6260
533-558	2	930	1040-1066	1	6895
610-634	1	1905	1067-1091	1	8936
635-659	2	1451	1092-1117	2	6758
660-685	1	1134	1118-1142	1	6940
686-710	1	1633	1143-1167	1	9979
737-761	2	2313	1168-1193	1	7257
761-786	3	1950	1194-1218	1	10433
838-863	2	3175	1270-1294	1	11340
940-964	1	3311	1880-1904	2	70988

Table 16. Total length-weight relationship of paddlefish. Lengths are in mm and weights in gm (from Carlander 1969).

TL	No.	Mean Wt.	Range
76-101	3	5	-
152-177	1	7	-
178-202	8	36	14-36
208-228	6	18	14-18
	2	26	-
229-253	14	27	23-36
254-278	25	36	32-45
	5	68	59-86
279-304	19	50	45-59
	7	100	86-127
305-329	11	59	50-73
	7	127	113-141
330-355	5	100	73-136
	2	154	-
356-380	2	200	-
381-405	1	136	-
	1	227	-
406-431	1	177	-
	1	254	-
432-457	3	200	181-213
458-482	2	249	227-272
	2	322	281-363
483-507	2	240	227-254
508-532	10	281	227-363
	1	399	-
533-558	6	426	-
	3	553	481-590
559-583	5	345	272-454
	2	726	680-771
584-609	19	508	454-613
	3	735	481-907
610-634	12	568	454-680
635-659	15	671	318-1089
660-685	15	726	567-907
	4	998	821-1179
686-710	7	857	680-1043
	8	1103	853-1497
711-736	13	1052	680-1406
737-761	8	1125	953-1497
	6	1511	1161-1874
762-786	30	1107	907-1361
	10	1715	1220-2631
	1	1950	-
787-812	4	1243	1021-1451
	7	1669	1361-2096
813-837	4	1451	1225-1905
	15	1887	1420-2767
838-863	3	1474	1248-1814
	12	1950	1565-2676
864-888	3	1987	1588-2223
	16	2291	1729-2722
889-913	6	1850	1474-2041
	22	2318	1814-3606
914-939	31	2571	2041-3343
940-964	31	2849	2354-4264
965-1015	95	3066	1928-5049
1016-1066	57	4042	2948-6350
1069-1117	42	4904	3402-7938
1118-1167	29	5475	4082-7484
1168-1218	20	6858	5216-8800
1219-1269	13	8128	6350-11140
1270-1320	8	9707	8391-11567
1321-1399	5	11998	8165-16216
1372-1410	4	12673	9979-18597
1422-1453	3	16974	14061-18597
1778	1	35834	-
1880	2	62052	56020-68040
2210	1	31751	-
2235	1	56020	-

Table 17. Length-weight equations for paddlefish (from Carlander 1969).

Location	Length Range	Equation
Mississippi R., Indiana	533 - 1270 mm TL[1]	log W = -4.975 + 2.842 log TL
Missouri R., S. Dakota	406 - 1524 mm TL	log W = -6.815 + 3.464 log TL
Fort Gibson Reservoir, Oklahoma	432 - 1194 mm TL	log W = -6.248 + 3.284 log TL
Alabama	610 = 1321 mm TL	log W = -7.896 + 3.81 log TL

[1]TL = Total length

Table 18. Coefficients of condition (K) reported for paddlefish (from Carlander 1969).

Location	No.	Length Range	Coefficient of Condition[1] Average	Range	Comments
South Dakota	47	457 - 1041mm	0.32	-	K value increased with increase in length of males but not females
Mississippi R., Indiana	245	406 - 1346mm	0.34	0.25 - 0.72	No increase in K value with increase in length
Missouri R., Indiana	204	406 - 1778mm	0.37	0.19 - 0.67	Some increase in K value with increase in length
Alabama	-	203 - 900mm		0.21 - 0.31	
		914 - 1332mm		0.29 - 0.52	

[1]Based on total lengths

Table 19. Stomach contents of paddlefish reported by Eddy and Simer (1929).

Location	Date	Major Items (% Volume)	Other Items
McIntyre Lake, Mississippi	March[1]	68% *Cyclops bicuspidatus* 20% *Daphnia longispina*	*Bosmina longispina*, cladoceran eggs, *Chydorus sphaericus*, *Synedra*
	April[1]	60% *Cyclops bicuspidatus* 20% *Diaptomus stagnalis* 10% *Bosmina longispina* 8% detritus	*Chydorus sphaericus*, protozoans, algae
	August[2]	80 - 90% *Cyclops leuckarti* and *Corethra* larvae	Mosquito larvae, cladocerans and small, generally immature *Cyclops bicuspidatus* were common but rarely abundant. Scarce items included rotifers, larval copepods, protozoa, and algae
Illinois River	June[3]	almost 90% *Cyclops bicuspidatus*	Other copepods, cladocerans, and cladoceran eggs, a few ostracods and one chironomid larvae were found. Small forms, eg. rotifers and algae, were rare.

[1] only one stomach examined.

[2] based on 26 stomachs.

[3] 10 stomachs examined.

that paddlefish fed in vegetation or on the bottom. Insect eggs constituted the bulk of this collection (78%), detritus was abundant (20%), and ostracods, *Bosmina* and *Chydorus sphaericus* comprised the remainder of the collection.

Sprague (1959) reported that *Daphnia* and *Diaptomus* comprised most of the food in 155 adult paddlefish collected in the winter in South Dakota and that phytoplankton was less abundant proportionately in the food than in the water. Ballard and Needham (1964) found that paddlefish fry chased *Daphnia* but not copepods. Hoopes (1960) found that cladocerans, copepods and algae were significant food items of paddlefish in the Mississippi River, primarily in late summer and fall.

Eddy and Simer (1929) gave an example of the prodigious amounts of plankton sometimes consumed by large paddlefish. The largest stomach they examined had a capacity of 700 cubic centimeters (cc). Well-filled stomachs from paddlefish taken in McIntyre Lake contained 80 *Corethra* larvae and 300 *Cyclops leuckarti* per cc. Thus, they calculated that a stomach with a 700 capacity would contain 56,000 *Corethra* larvae and 210,000 *C. leuckarti*.

Hoopes (1960) found that mayfly naiads *(Hexagenia sp.)* comprised 46% of the volume of food of 64 paddlefish examined from the Mississippi River. Meyer (1960) also reported that mayfly naiads were a major food item of adult paddlefish in the Mississippi River (Carlander 1969). The presence of large volumes of mayfly naiads in paddlefish stomachs indicates the occurrence of bottom feeding by these fish.

Eddy an Simer (1929) concluded that due to the structure of the gill raker and alimentary canal paddlefish "obviously cannot eat other fish." Further, no fish remains were found in about 300 stomachs of paddlefish netted in Norris Reservoir, Tennessee, in 1958 (Fitz 1966). However, Forbes (1888) indicated that paddlefish may feed to a very small extent on fish. Fitz (1966) noted several reports of Osage River paddlefish being taken on hooks baited with minnows in 1958 and 1959. Meyer (1960) reported a 64 mm river darter, *Percina shumardi*, in one paddlefish stomach. The stomach of a paddlefish 30.5 inches long and 4.3 lb. in weight, taken in the Tennessee River, contained 13 threadfin shad *(Dorosoma petenense)*, 2 to 4 inches long (Fitz 1966). Fitz (1966) noted that the shad were in various stages of decomposition indicating that they were taken at different times, and concluded that it was unlikely that this many shad would have been consumed merely by accident.

The role of the paddle in feeding, if any, is uncertain. Beach (1902) concluded that the paddlefish is largely "vegetative" in its habits and that the paddle is used to manipulate and guide water plants into its mouth. However, no other studies support Beach's conclusions. Swimming movements of paddlefish involve lateral movements of the paddle (Eddy and Simer 1929). It was suggested that these lateral movements may aid in jarring loose aquatic animals from vegetation (Norris 1923). Eddy and Simer (1929) observed that lateral movements of the paddle occurred while swimming through water void of vegetation and concluded that this movement does

not represent a special modification for securing food. Jordon and Evermann (1896), Imms (1904), Stockard (1907), Alexander (1914) and Norman and Greenwood (1963) asserted that the paddle is used for stirring up bottom mud, thus suspending bottom fauna in the water from which they are strained by the gill rakers.

Parasites and predators - Purkett (1963) indicated that paddlefish are heavily parasitized by the cestode *Marsipometra hastata* Linton. Meyer (1960) stated that these parasites do not appear to harm the fish seriously. Hugghins (1972) examined a single 19 inch paddlefish from South Dakota. It was infected with *Marsipometra hastata*, the nematode *Camallanus oxycephalus*, and an unidentified species of nematode. Eddy and Simer (1929) reported that paddlefish were usually infected with many nematodes and that most individuals contained cestodes, sometimes over a thousand per fish, but that trematodes were rare except for a very common gill polystome. They described three species of *Marsipometra* occurring in different regions of the digestive tracts of paddlefish.

Paddlefish are probably relatively unimportant as prey for other fishes since they are too large to be preyed upon by most fishes after their first year (Purkett 1963), and they are usually not extremely abundant.

Summary

Paddlefish inhabit the open waters of large silty rivers, oxbows, bayous, flood-plain lakes, and reservoirs.

They are apparently highly migratory, migrating mostly near the surface. They occur in the headwaters of the Lake of the Ozarks in late February. In spring, they migrate upstream to spawning sites in the Osage River when water temperatures warm to near 50°F and water levels rise due to heavy rains. Spent fish return to the lake immediately after spawning.

Paddlefish spawn from March to June. In the Osage River and its tributaries, paddlefish spawn in mid to late April and possibly in early May at water temperatures above 50°F or more feet above normal. Spawning occurs in running water over sand and pebbles or small gravel. Spawning has been observed in late afternoon or evening.

The smallest mature males and females reported weighed 2270 and 2950 gm, respectively. Males first mature at an age of about 7 years and at lengths of about 1067 mm. Paddlefish might have a periodicity in their sexual maturation. Females may spawn at intervals of 4 to 7 years. Two females 1374 mm long contained 137,247 and 141,531 eggs.

Fertilized paddlefish eggs are adhesive and range from 2.7 to 4.0 mm in diameter. Viability is greater among eggs attached to gravel than among loose eggs. Eggs incubating on gravel bars in the Osage River were often subject to desiccation due to falling water levels. Eggs hatch in 7 days or less at water temperatures of 65 to 70°F.

Newly hatched fry are 8.0 to 9.5 mm in total length. In the Osage River, continuous swimming after hatching caused most fry to be swept to deep water before desiccation due to falling water levels occurred.

The largest reported paddlefish was 1524 mm long and weighed 83.5 kg. Paddlefish aged 30 years have been collected.

Paddlefish feed largely upon plankton, straining the larger plankton species from the water with their gill rakers. Copepods, cladocerans and *Corethra* larvae comprise the bulk of the plankton species consumed. The occasional occurrence of large vo.. of mayfly naiads in paddlefish stomachs indicates that paddlefish also feed on the bottom. Paddlefish may also rarely feed upon other fish since a river darter and 13 threadfin shad have been found in two paddlefish stomachs.

The cestode *Marsipometra hastata* is a common parasite of paddlefish. Paddlefish are also frequently parasitized by nematodes.

LIFE HISTORIES OF THE SHOVELNOSE AND PALLID STURGEONS

Introduction

Two species of *Scaphirhynchus* occur in North American freshwater; *S. platorynchus* (Rafinesque), the shovelnose sturgeon, and *S. albus* (Forbes and Richardson), the pallid sturgeon. The shovelnose sturgeon is found mainly in the Mississippi, Missouri and Ohio rivers and their tributaries, but apparently ranges from the Hudson Bay drainage of the Canadian Plains southward to New Mexico, Arkansas and Kentucky (Eddy and Surber 1947, Held 1969). Held (1969) noted that the distribution of this species in the Missouri River has been limited by the construction of reservoirs. The pallid sturgeon is rare in the upper Mississippi River and its larger tributaries (Carlander 1969). Carlander (1969) indicated that this species is fairly common in the Missouri River and its new reservoirs. However, Benson (1968) listed the pallid sturgeon as being rare in Missouri River mainstem reservoirs. Walburg (1964) reported that only 17 pallid sturgeon were captured during 7 years of study of Lewis and Clark Lake, a mainstem reservoir on the Missouri River. Over a thousand shovelnose sturgeon were captured in this reservoir during the same period.

The existing literature on the life histories of the shovelnose and pallid sturgeons is reviewed here. Information on these species, especially the pallid sturgeon, is scanty. Information on other species of sturgeon is noted for aspects of the life histories of these species which have not been described.

The Life Histories of the Shovelnose and Pallid Sturgeons

Habitat - Gowanloch (1933) reported that shovelnose sturgeons show a strong preference for current. Before ponding of the Ohio River began, shovelnose sturgeon in this river apparently fed mainly "over the clean sand and gravel bottoms of chutes and bars, or wherever there was considerable current and a clean bottom" (Trautman 1957). In Ohio, they appear to avoid tributary streams (Trautman 1957). Cross (1967) noted that shovelnose sturgeon in Kansas "live near the bottom in large rivers, most often over firm, shallow, sandy bottoms in channels where the current is strong." Held (1969) stated that shovelnose sturgeon are "restricted to a lotic environment, particularly to the larger rivers except at times of spawning when they may enter some of the tributaries." In Lewis and Clark Lake, shovelnose sturgeon are collected mainly from the old river channel in the upper reaches of the reservoir (Walburg 1964, Held 1969). The abundance and condition of shovelnose sturgeon declined after the impoundment of Lewis and Clark Lake (Walburg 1964, Sprague 1960).

Pallid sturgeon apparently inhabit only the largest, muddiest rivers of the Missouri - Mississippi system (Cross 1967). Like the shovelnose sturgeon, they occur most often over firm sandy bottoms in strong currents in Kansas (Cross 1967). Unlike the shovelnose sturgeon, pallid sturgeon in Kansas do not penetrate far into the secondary streams of the Missouri system nor do they inhabit the less turbid large rivers north and east of the Missouri River (Cross 1967).

Spawning - Trautman (1957) reported that, prior to ponding in about 1910, spawning runs of shovelnose sturgeon occurred in the Ohio River in late February and March when the river was rising. Shovelnose sturgeon with freely running eggs and milt have been found in Kansas in late April and in Iowa in mid-May (Gowanloch 1933, Cross 1967). Forbes and Richardson (1920) and Carlander (1969) reported that shovelnose sturgeon spawn between April and June. In South Dakota, they spawn prior to June 20 or in late June and early July (Carlander 1969).

Forbes and Richardson (1920) and Gowanloch (1933) suggested that shovelnose sturgeon probably ascend smaller streams to spawn. In the Mississippi River near Keokuk, Iowa, they spawn on rocky bottoms in swift water (Coker 1930).

Cross (1967) noted concentrations of shovelnose sturgeon below a low dam on the Kansas River in spring and concluded that migrations upstream precede spawning. He reported that these concentrations seemed greatest in high water years and least in times of drought. Conversely, Coker (1930) reported that spring runs of sturgeon in the Mississippi River at Keokuk are best when the river is low in spring and poor when it is high. Cross suggested that shovelnose sturgeon may seek "an optimal volume of flow, departing from the largest rivers to enter tributaries for spawning in years when stream are high." Gowanloch (1933) noted that shovelnose sturgeon seem to swim near the surface during their spawning migrations.

Virtually nothing is known of the spawning activities of pallid sturgeon. Gowanloch (1933) reported that the white shovelnose sturgeon, *Parascaphirhynchus albus*, spawned from June 1 to August 1. *P. albus* is apparently a synonym of *S. albus*, the pallid sturgeon (Barnickol and Starrett 1951).

Sexual maturity - Cross (1967) reported that male and female shovelnose sturgeon are sexually mature at lengths of about 20 and 25 inches (508 and 635 mm), respectively. Carlander (1969) indicated that males and females mature at 551 and 645 mm, respectively. Shovelnose sturgeon over 508 mm long in Oahe Reservoir, South Dakota, were considered mature (Carlander 1969). Helms (1974) reported two mature males 22.0 inches (559 mm) long from the Mississippi River in Iowa. Barnickol and Starrett (1951) found that male shovelnose sturgeon mature at lengths of 19.5 to 22 inches (from the tip of the snout to the base of the caudal filament) in the Mississippi River between Caruthersville, Missouri, and Dubuque, Iowa. The smallest mature female they examined was 25 inches long. The smallest mature males and females examined by Monson and Greenbank (1947) measured 495 and 521 mm in fork length, respectively. In Fort Randall Reservoir, South Dakota, the smallest mature males and females found were 356 mm in total length (Shields 1956). Spencer (1971) indicated that shovelnose sturgeon may be mature at weights of 2 lb or less.

Shovelnose sturgeon in Pool 13 of the Mississippi River apparently mature in age group IV or, rarely, age group III

(Helms 1974). The size of first maturity of shovelnose sturgeon in Oahe Reservoir (508 mm) corresponds to an age of over 10 years (see Table 21). However, Helms (1974) suspected that Fogle (1963) included false annuli when aging shovelnose sturgon from Oahe Reservoir. Thus, an age of first maturity of less than 10 years is probable for Oahe Reservoir shovelnose sturgeon.

In Oahe Reservoir, male pallid sturgeon mature at total lengths of 533 to 584 mm (21.0 - 23.0 inches) (Carlander 1969). This corresponds to an age of about 4 years (see Table 21), assuming that Fogle's (1963) aging of pallid sturgeon was accurate.

Fecundity and early development - The fecundity and early development of shovelnose and pallid sturgeons are unknown. Scott and Crossman (1973) reported fecundities of 49,835 to 667,472 eggs per female for lake sturgeon 11.5 to 112.0 pounds in weight; 800,000 to 2,400,000 eggs per female for Atlantic sturgeon; and 699,000 to 3 to 4 million eggs per female for white sturgeon. Lesser fecundities can be expected for shovelnose and pallid sturgeons since they usually do not attain the large size reported for mature lake, Atlantic and white sturgeons.

Scott and Crossman (1973) reported egg diameters of 2.5 - 2.6 and 2.7 - 3.3 mm for Atlantic and lake sturgeons, respectively. They noted incubation times of 5 to 8 days at 60 - 64°F for lake sturgeon and of about one week at 64° for Atlantic sturgeon. Newly hatched lake and Atlantic sturgeon fry are about 8 and 11 mm long, respectively (Scott and Crossman 1973).

Growth - A young-of-the-year shovelnose sturgeon captured June 24 in Pool 13 of the Mississippi River measured 2.2 inches (56 mm) (Helms 1974). Young-of-the-year shovelnose sturgeon ranged from 7.4 to 9.9 inches (188 to 251 mm) by the end of October (Helms 1974).

Table 20 shows the length-weight relationships of shovelnose sturgeon. Helms (1974) described this relationship with the equation log W = -4.292 + 3.307 log FL for shovelnose sturgeon in age groups 0 - III Pool 13 of the Mississippi River.

Condition factors averaged 11.6 and ranged from 9 to 17 for the shovelnose sturgeon examined by Helms (1974). Carlander (1969) reported coefficients of condition K, (TL), averaging 0.25 and ranging from 0.22 to 0.27 for 635 shovelnose sturgeon 305 to 787 mm in total length from Fort Randall and Gavins Point reservoirs, South Dakota. He indicated that the K values decreased slightly from June to September and that they exhibited no differences between sexes or trend with size.

Table 21 displays the lengths for each year of life of shovelnose sturgeon in the Mississippi River (Helms 1974) and Oahe Reservoir, South Dakota (Fogle 1963). The sturgeon examined by Helms (1974) were in age groups 0 - III and ranged from 7.4 - 23.7 inches in fork length and 0.6 - 2.02 pounds in weight. The shovelnose sturgeon studied by Fogle (1963) were 18 - 23 inches in total length (16 - 20.5 inches in fork length) and up to 10 years old. Zweiacker (1967) examined 288 shovelnose sturgeon from the Missouri River aged 8 to 27 years and ranging from 18 to 22 inches in fork length. The sturgeon in all three

Table 20. Length (mm) - weight (gm) relationships of shovelnose sturgeon from locations on the Mississippi, Missouri and Ohio rivers. (from Carlander,1969).

Mississippi R.			Ohio R.				Weight (gm)		
FL	No.	Mean Wt.	No.	Mean Wt.	Range	Total length (mm)	Oahe Reservoir (1313 fish)	Ft. Randall and Gavins Point Reservoir (587 fish)	Upper Mississippi River
406-431	3	281	1	454	-	279-304	50	-	-
432-456	12	295	-	-	-	305-329	82	64	86
457-482	17	376	2	567	-	330-355	104	86	127
483-507	28	499	3	567	-	356-380	122	104	172
508-532	57	562	6	662	567-680	381-405	145	136	213
533-558	52	644	12	789	680-907	406-431	181	168	249
559-583	96	762	7	857	680-907	432-456	222	213	318
584-609	87	902	2	1188	1134-1248	457-482	277	249	372
610-634	96	1038	9	1197	1021-1361	483-507	318	290	454
635-659	113	1239	6	1252	1021-1474	508-532	386	336	522
660-685	126	1465	9	1511	1361-1814	533-558	454	390	654
686-710	90	1647	3	1665	1361-1814	559-583	513	468	766
711-736	57	1896	1	1928	-	584-809	622	567	867
737-761	27	2186	1	2155	-	610-634	671	635	998
762-786	12	2540	-	-	-	635-659	839	699	1143
787-812	4	2681	-	-	-	660-685	993	780	1420
						686-710	-	843	-
						711-736	-	921	1928
						737-761	-	1206	2019
						762-786	-	1297	-
						787-812	-	1397	-

Table 21. Lengths for each year of life of shovelnose and pallid sturgeons.

Species	Source			Year of Life									
				1	2	3	4	5	6	7	8	9	10
Shovelnose Sturgeon	Helms (1974)	Fork Length	(mm)	226	348	480	559	-	-	-	-	-	-
			(inches)	8.9	13.7	18.9	22.0	-	-	-	-	-	-
		Number		9	59	22	20	-	-	-	-	-	-
	Fogle (1963)	Total Length	(mm)	213	274	325	366	399	437	470	483	457	503
			(inches)	8.4	10.8	12.8	14.4	15.7	17.2	18.5	19.0	18.0	19.8
		Number		35	35	35	31	23	17	9	6	2	1
Pallid Sturgeon	Fogle (1963)	Total Length	(mm)	279	378	470	574	638	673	732	790	838	881
			(inches)	11.0	14.9	18.5	22.6	25.1	26.5	28.8	31.1	33.0	34.7
		Number		6	6	6	6	6	5	5	4	3	2

studies were aged using sectioned fin rays. The growth rates reported by Fogle (1963) and Zweiacker (1967) are much slower than that reported by Helms (1974). Helms (1974) suspected that the earlier studies were in error due to the inclusion of false annuli. However, he noted that the possibility of such instances of slow growth is supported by tagging studies. Tagged sturgeon in Red Cedar River, Wisconsin, and the Missouri River near Vermillion, South Dakota, grew only a few millimeters each year and often exhibited negative growth. Helms noted, however, that tagging retarded growth among some fishes. Helms (1973) examined shovelnose sturgeon in 6 pools of the Mississippi River. The oldest fish found was estimated at 12 years old and measured 28.2 inches in fork length. Helms (1973) attributed reduced growth after the fourth year of life mostly to sexual maturity.

Spencer (1971) stated that shovelnose sturgeon are the smallest sturgeons in Alabama, seldom exceeding weights of 8 pounds. Gowanloch (1933) reported that 41 male and 21 female shovelnose sturgeon averaged 21 inches long and almost 2 pounds and 25.5 inches long and 3¼ pounds, respectively. In Ohio, shovelnose sturgeon are usually 18.0 to 30.0 inches long and 1 to 5 pounds in weight (Trautman 1957). The largest specimen reported by Trautman (1957) was 32.0 inches long and weighed 10 pounds. Cross (1967) noted that the maximum size normally attained by shovelnose sturgeon in Kansas is about 30 inches and 5 pounds, although specimens as large as 7 pounds have been reported. Shovelnose sturgeon caught in Lewis and Clark Lake ranged from

13.0 to 31.0 inches in length, excluding the caudal filament, and averaged 0.6 pounds in weight (Walburg 1964).

The length-weight relationship of pallid sturgeon is shown in Table 22. Table 23 summarizes the coefficients of condition, K (TL), reported for pallid sturgeon. Carlander (1969) noted that the K values generally increase with increase in length of pallid sturgeon. Table 21 shows the lengths for each year of life of pallid sturgeon in Oahe Reservoir. The growth rate of pallid sturgeon in this reservoir is apparently much faster than that of shovelnose sturgeon in the same area but only slightly faster than that of the shovelnose sturgeon from the Mississippi River examined by Helms (1974).

Unlike shovelnose sturgeon, pallid sturgeon often attain relatively large sizes. Seventeen pallid sturgeon captured in Lewis and Clark Lake ranged from 3.5 to 18.8 pounds in weight and 26 to 51 inches in length, excluding the caudal filament (Walburg 1964). Brown (1955) reported a 47 pound sturgeon from the Missouri River near Fort Benton, Montana, a 31.5 pound, 58 inch (total length) pallid sturgeon from Fort Peck Reservoir, Montana, and a pallid sturgeon 66 inches in total length and 38 pounds in weight from the Tongue River near Miles City, Montana. Walburg (1964) noted that a pallid sturgeon weighing over 68 pounds was caught in the Missouri River in North Dakota.

Food habits - Held (1969) described the mode of feeding of sturgeons as suctorial on benthic organisms. Cross (1967)

Table 22. Length-weight relationship of 71 pallid sturgeon from Oahe Reservoir, South Dakota (from Carlander 1969)

Total Length (mm)	Weight (gm)
470	249
495	299
521	354
546	417
572	499
648	749
673	834
724	1089
749	1216
800	1588
826	1742
851	1964
876	2195
902	2440
927	2745
978	3266
1003	3547
1029	3932
1054	4196
1080	4427
1156	6174

Table 23. Coefficients of condition, K (TL), of pallid sturgeon (from Carlander, 1969)

Location	No.	Total Length (mm)	Weight (gm)	K(TL)
Oahe Reservoir	76	457 - 1143	-	0.27 - 0.35
Gavins Point Reservoir	12	660 - 1295	1588 - 8505	0.27 - 0.42

observed shovelnose sturgeon searching for food in aquaria by raking the bottom with the barbels on their snouts.

Cross (1967) indicated that shovelnose sturgeon are mainly insectivorous, but eat some algae and bits of higher aquatic plants. Eddy and Suber (1947) found dragonfly naiads in the stomachs of shovelnose sturgeon. The stomachs of shovelnose sturgeon caught in the Mississippi River at Andalusia, Illinois, contained mayfly naiads *(Hexagenia sp.)* (Barnickol and Starrett 1951). Hoopes (1960) reported that the stomach contents of 74 shovelnose sturgeon caught in the Mississippi River near Keokuk, Iowa, were 75% caddisfly larvae (68% *Potamyia flava* and 7% *Cheumatopsyche campyla*), 17% *Hexagenia* naiads and 8% other material including immature Plecoptera, Diptera and Odonata. Held (1969) found that aquatic insect larvae, crustaceans and terrestrial insects were the main food items of shovelnose sturgeon in the Missouri River 33 km above and 37 km below the Gavins Point Dam in June, 1962 (see Table 24). Tendipedidae, Heleidae (Mostly *Palpomyia sp.*), Baetidae (Mostly *Caenis sp.*), Coleoptera, Odonata and *Daphnia* comprised 29.2, 22.3, 8.8, 7.5, 6.0 and 3.9 percent, respectively, of the volume of food organisms of these sturgeon.

Held (1969) noted that the frequency of occurrence of zooplankters, mainly cladocerans, in shovelnose sturgeon stomachs was 68% and that many cladocerans were sometimes found in a single stomach. He suggested that the sturgeon's feeding habits may thus occasionally be of a grazing nature. He also suggested that the preference of shovelnose sturgeon for lotic

Table 24. Stomach contents of 75 shovelnose sturgeon collected from the Missouri River, June, 1962 (from Held 1969).

	Digestive tract with food item (Frequency of occurrence)		Total organisms		Total volume of food item	Percentage of total volume	
	Number	Percent	Number	Percent	Milliliters	Of all contents	Of all orgamisms
Empty	2	2.7					
Aquatic organisms							
Insecta							
Diptera							
Tendipedidae-L	73	97.3	36,743	63.9	12.42	16.7	29.2
Heleidae-L	70	93.3	12,915	22.5	9.49	12.7	22.3
Dipteran pupae	67	89.3	1,403	2.4	1.33	1.8	3.1
Other	57	76.0	534	.9	1.74	2.3	4.1
Ephemeroptera							
Baetidae-N	58	77.3	1,057	1.8	3.76	5.1	8.8
Heptageniidae-N	31	41.3	70	.1	.92	1.2	2.2
Other	30	40.0	212	.4	.78	1.0	1.8
Coleoptera	22	29.3	129	.2	3.21	4.3	7.5
Odonata	28	37.3	97	.2	2.54	3.4	6.0
Trichoptera	32	42.7	154	.3	1.07	1.4	2.5
Other Insecta	13	17.3	18	T	.30	.4	.7
Total aquatic Insecta	73	97.3	53,331	93.0	37.56	50.5	88.1
Crustacea							
Cladocera	32	42.7	2,393	4.2	1.67	2.2	3.9
Other	44	58.7	1,099	1.9	.28	.4	.7
Other aquatic organisms	51	68.0	432	.7	.18	.2	.4
Total aquatic organisms	73	97.3	57,255	99.6	39.69	53.4	93.1
Terrestrial organisms							
Total terrestrial Insecta	29	38.7	141	.2	1.32	1.8	3.1
Arachnoidae	7	9.3	21	T	.76	1.0	1.8
Chilopoda	9	12.0	43	.1	.86	1.2	2.0
Total terrestrial organisms	30	40.0	205	.4	2.94	4.0	6.9
Inorganic matter	60	80.0			8.17	11.0	
Plant material	6	8.0			.09	.1	
Organic debris	72	96.0			23.45	31.5	
Total number of organisms			57,460				
Total volume of organisms					42.63		
Total volume of all contents					74.34		

environments may be related to reduced siltation and the resulting greater accessibility of benthos, their main food items.

The food habits of pallid sturgeon are poorly known. A pallid sturgeon 27.5 inches long and 1.5 lbs. in weight, caught in the Mississippi River near Keokuk, contained small quantities of insect fragments and minnows in its stomach and intestine (Gowanloch 1933). The stomachs of a few specimens from the Kansas River contained insect larvae and small fishes (Cross 1967).

Parasites and predators - Hoffman (1967) listed the trematodes *Crepidostomum lintoni* and *Pristotrema manteri*, the nematode *Ascaris scaphirhynchi* and the leech *Placobdella montifera* as the parasites of shovelnose sturgeon. Nickerson and Hutchison (1971) isolated the fungus *Basidiobolus ranarum* from shovelnose sturgeon in Arkansas and Missouri. They noted that this fungus has been suspected as a pathological agent in humans. Hubley (1961) reported lamprey parasitism of shovelnose sturgeon in the upper Mississippi River. No reports of parasitism upon pallid sturgeons were found.

No records of predation upon shovelnose or pallid sturgeon were found. Harkness and Dymond (1961) noted that there is no evidence that adult lake sturgeon are attacked by predators and that their large size makes such attacks unlikely. They admitted that the young may be preyed upon by larger fishes but noted that there are no records of such predation.

Summary

Shovelnose sturgeon inhabit large rivers, apparently preferring areas with strong currents and firm sandy or gravel bottoms. They appear to avoid tributary streams, except possibly during the spawning season. Pallid sturgeon apparently inhabit only the largest, muddiest rivers of the Missouri-Mississippi system, occurring most often over firm sandy bottoms in strong currents.

Shovelnose sturgeon spawn between April and early July. They may ascend small streams, spawning on rocky bottoms in swift water. Upstream migrations precede spawning. Pallid sturgeon spawn between June 1 and August 1.

The smallest mature male and female shovelnose sturgeon reported were 356 mm long and were caught in Fort Randall Reservoir, South Dakota. Other reports indicate that male and female shovelnose sturgeon mature at lengths of 495 - 559 mm and 508 - 645 mm, respectively, and at weights of as little as 2 pounds. In Pool 13 of the Mississippi River, shovelnose sturgeon mature in age group IV or, rarely, age group III. In Oahe Reservoir, the size of first maturity of shovelnose sturgeon corresponds to an age of over 10 years, but this age may be overestimated due to the inclusion of false annuli. Male pallid sturgeon in Oahe Reservoir mature at total lengths of 533 - 584 mm, corresponding to an age of about 4 years.

The fecundity and early development of shovelnose and pallid sturgeons are apparently unknown. Atlantic and lake sturgeons have egg diameters of 2.5 - 2.6 and 2.7 - 3.3 mm,

respectively. Newly hatched lake and Atlantic sturgeons measure about 8 and 11 mm in length, respectively.

In Pool 13 of the Mississippi River, young-of-the-year shovelnose sturgeon measure 56 mm in late June and 188 - 251 mm by the end of October. The length-weight relationships and lengths for each year of life of shovelnose and pallid sturgeons are shown in Table 20, 21, and 22. Rapid growth rates are reported for young shovelnose sturgeon in the Mississippi River where fish in age group 0 - III ranged from 7.4 - 23.7 inches in fork length. Growth rate decreased after the fourth year of life apparently due to the onset of sexual maturity. Slow growth rates reported for shovelnose sturgeon in Oahe Reservoir, and the Missouri River might be the result of inaccurate ageing. In Oahe Reservoir, pallid sturgeon appear to grow much faster than shovelnose sturgeon.

Adult shovelnose sturgeon usually range from 18.0 -30.0 inches in length and 1 - 5 pounds in weight. Shovelnose sturgeon caught in Lewis and Clark Lake averaged only 0.6 pounds in weight. The largest specimen reported was 32.0 inches long and weighed 10 pounds. Pallid sturgeon from Lewis and Clark Lake ranged from 26 - 51 inches in length and 3.5 - 18.8 pounds in weight. A pallid sturgeon weighing over 68 pounds was caught in North Dakota.

Shovelnose sturgeon feed primarily on benthos. Aquatic insect larvae, mainly Tendipidae, Heleidae, caddisfly larvae,

mayfly naiads or dragonfly naiads, are their most important food items. A high frequency of occurrence of cladocerans in shovelnose sturgeon stomachs in some areas suggests that this sturgeon feeding habits might occasionally be of a grazing nature. The few pallid sturgeon stomachs examined contained insect fragments and small fishes.

The parasites of shovelnose sturgeon include two trematodes, a nematode, a leech, lampreys, and the fungus *Basidiobolus ranarum,* a suspected human pathogen. No reports of parasitism upon pallid sturgeon or predation upon shovelnose or pallid sturgeons were found.

LIFE HISTORY OF THE SHORTNOSE GAR

Introduction

The shortnose gar, *Lepisosteus platostomus* (Rafinesque), occurs from South Dakota to the Ohio Valley and south to Alabama and Texas (Priegel 1963). Greene (1935) reported it in Wisconsin only from the Mississippi drainage. However, Priegel (1963) reported a specimen taken from Lake Winnebago, in the Great Lakes drainage in Wisconsin. Becker (1964) subsequently reported additional specimens from Lake Winnebago. Priegel (1963) concluded that the dispersal of shortnose gar from the Mississippi drainage probably occurred by way of the Wisconsin River, through the canal at Portage into the Fox River of the Great Lakes drainage and eventually into Lake Winnebago.

In addition to the shortnose gar, four other species of gar are recognized in North America: the alligator gar, *L. spatula*, the longnose gar, *L. osseus* the spotted gar, *L. oculatus*, and the Florida gar, *L. platyrhincus*. The spotted and shortnose gars were long confused and both referred to as *L. platostomus* (Scott and Crossman 1973). Taxomomic separation of the two forms occurred about 1940 (Lagler *et al.* 1942). The Florida gar *(L. platyrhincus)* is also very similar to the latter two species and was considered by Hunt (1952) to be the Florida representative of the spotted gar.

This section reviews the literature on the life history of the shortnose gar, *L. platostomus*. Some aspects of the life history of this species have not been described. In these cases,

information for other species of gar, especially the similar spotted and Florida gars, is noted.

The Life History of the Shortnose Gar

Habitat and movements - Trautman (1957) indicated that the largest populations of shortnose gar in Ohio occur in lowland lakes, oxbows and backwaters and the smaller populations inhabit the still waters of the pools of rivers. He noted that shortnose gar apparently avoid strong currents and thus streams of high gradient and that they are not found among rooted aquatic vegetation as often as is the spotted gar. Shortnose gar seem to prefer clear waters, possibly because they feed by sight, but they inhabit silt-laden rivers sparingly in Ohio (Trautman 1957).

Cross (1967) described a very different distribution for shortnose gar in Kansas. He noted that they usually avoid the quiet backwaters, oxbows and impoundments that are often occupied by spotted and longnose gars. Cross indicated that following a period early in life spent in shallow backwaters, shortnose gar move into the deeper water and stronger currents of the mainstreams of rivers in Kansas.

Taber (1969) reported that young gar in Lake Texoma, Oklahoma, prefer shallow calm water near emergent vegetation often occurring within inches of shore, and move further from shore as their size increases. Echelle and Riggs (1972) found that gar sac-fry in Lake Texoma tended to remain in the area of egg deposition and occurred in locally dense populations attached to submerged objects. After absorption of the yolk-sac,

fry became more dispersed, but several could be found together in areas of cover and protection from heavy wave action (Echelle and Riggs 1972). Taber (1969) observed aggregations of 5 to 10 fry (about 20 mm long) around a small emergent plant near shore in Lake Texoma but reported that individuals longer than about 25 mm were usually solitary. Echelle and Riggs (1972) and Gowanloch (1933) concurred that gar fry do not show a pronounced tendency to school. Echelle (1968) suggested that young longnose gar prefer shallow waters and that there is no daily migration to and from the shallows. Echelle and Riggs (1972) indicated that these conclusions seem to apply to young gar in general.

Becker (1964) captured adult shortnose gar (467 to 558 mm in total length) in water less than 1.5 feet deep between large beds of submergent aquatics in Lake Winnebago. Electrofishing showed that adult shortnose gar are more abundant in shallow waters in Lake Texoma at night than during daylight hours (Echelle and Riggs 1972).

Seasonal variations in the distribution of *L. platostomus* have not been examined. However, Holloway (1954) described seasonal changes in the distribution of "shortnose" or Florida gar *(L. platyrhincus)* in Florida lakes and streams. From mid-February to mid-April large concentrations of gar occurred on shallow mud-flats in small lakes. These concentrations showed little relationship to the amount of aquatic vegetation or cover present. In the Oklawaha River, few Florida gar were taken from the mainstream channel and largest numbers were most often found at the mouths of old bayou channels and tributaries,

in bayou channels where a slight flow of water occurred, and in marginal vegetation, mostly lotus and water lilies. In mid-April, these gar concentrations gradually dispersed in the lakes and streams. Since peak spawning occurred about two months after dispersal, these concentrations apparently were not directly related to reproductive behaviour.

Echelle and Riggs (1972) reported that during daylight young gar spend much time resting motionlessly, usually in close association with submerged or overhanging objects near shore. At night, they commonly swim actively in shallow open waters. Echelle and Riggs (1972) noted that certain individuals were very localized in activity and were found in practically identical spots each day. They cited the example of a longnose gar that was found under the same overhanging limb from mid-July until its capture on September 1, 1965.

Gowanloch (1933)[1] indicated that"short-nosed" gar are known to move about in schools both before and after the spawning season but noted that evidence of any extensive seasonal migration is lacking. Holloway (1954) reported that Florida gar *(L. platyrhincus)* are gregarious and usually swim in groups of 2 to 10 or more.

Gowanloch (1933) stated that gars are quite tolerant of blackish and even completely salt water. Leim and Scott (1966) reported two longnose gar caught in the Saint Lawrence River where salinities usually varied from 13 to 20 ppt and were as high

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[1]Gowanloch probably does not distinguish between spotted *(L. oculatus)* and shortnose *(L. platostomus)* gars.

as 25 ppt on the bottom. Goodyear (1967) found that longnose and spotted gars were common in brackish waters along the Mississippi coast where salinities ranged from 3 to 10 and 2 to 10 ppt, respectively. Gowanloch (1933) indicated that "short-nosed" gar appear to be confined to freshwater.

Gars are able to supplement gill respiration with aerial respiration using the swim bladder. Aerial breathing effectively allows gars to operate independently of the dissolved oxygen content of their aquatic medium (Hill *et al.* 1973). De Roth (1973) suggested a thermal preferendum of 65 to 75°F for spotted gars.

Spawning season - Most gar spawning in Lake Texoma apparently occurs between early April and the end of May (Taber 1969, Echelle and Riggs 1972). Echelle and Riggs (1972) suggested that peak spawning activity occurred shortly after an abrupt warming trend in early spring in 1965.

In Illinois, shortnose gar spawn in May and June (Richardson 1913) or from May to August (Gowanloch 1933). Potter (1926) reported that shortnose gar spawn from May to July in Iowa. In South Dakota, shortnose gar spawned from May 30 to July 15 at water temperatures of 19 to 23.5°C (66.2 to 74.3°F) in 1956 in Fort Randall Reservoir (Shields 1957a) and in late June and early July in 1957 and 1958 in Gavins Point Reservoir (Shields 1958, Sprague 1959). Shortnose gar spawned during the last 2 weeks in June in Lewis and Clark Lake, South Dakota (Walburg 1964).

Echelle and Riggs (1972) observed spotted and longnose gars spawning at water temperatures between 68 and 86°F. Taber (1969) observed spotted gar spawning on April 9 at a water temperature of 61°F and noted that this species spawned earlier than other gars in Lake Texoma.

Spawning sites and behaviour - Richardson (1913) reported shortnose gar spawning in about 12 to 35 inches of water in Illinois. Gowanloch (1933) indicated that "short-nosed" gar spawning occurred in "weedy or willow grown waters" in Illinois. He noted that spawning shortnose gar ran in pairs, each female accompanied by a small male. Shields (1957b) observed shortnose gar spawning in the same general areas as carp in the Fort Randall Reservoir, South Dakota. In the reservoir, carp spawned in shallow grassy areas, usually at water depths of less than one foot.

In Lake Texoma, spotted gar spawned over dead vegetation and algal mats in quiet, weedy waters while longnose gar spawned over algae and bare rock along windswept shorelines and rocky points (Echelle and Riggs 1972).

Sexual maturity - Shields (1958) reported that a few male and female shortnose gar mature at lengths of 457 and 483 mm, respectively, in South Dakota. Walburg (1964) found that all shortnose gar over 20.0 inches (508 mm) long were mature in Lewis and Clark Lake.

Netsch and Witt (1962) found that, in Missouri, male longnose gar mature between 3 and 4 years of age while females probably mature at about 6 years of age.

Sex ratio - The sex ratios in shortnose gar populations have not been examined. Netsch and Witt (1962) reported sex ratios of 2.62, 2.25, 0.45, and 0.08 males per female for longnose gar in consecutive 5-year age intervals from age I to XX. The sharp decline in sex ratio with increasing age indicates a shorter life spawn for male than female longnose gar. Holloway (1954) reported sex ratios of 0.36, 0.58, 2.68 and 3.07 males per female for longnose gar in Florida. The smaller ratios were associated with larger,and thus presumably older, males and again suggest a shorter longevity for male than female longnose gar. The ratios of males to females in populations of Florida gar range from 0.43 and 0.56 in small Florida lakes to 0.81, 0.91 and 2.27 in creeks and rivers in Florida (Holloway 1954). The sex ratios reported for Florida gar appear to be unrelated to the average weight of fish in each population.

Fecundity - Potter (1926) reported a 4082 gm female shortnose gar with 36,460 eggs. No other information on the fecundity of *L. platostomus* was found.

Holloway (1954) reported fecundities for Florida and longnose gars. The fecundity of Florida gar (14 to 34 inches in total length) ranged from 1,125 to 15,450 eggs per female. A single female 13 inches long contained only 523 eggs. In general, the fecundity increased with length of the gar. A few individuals in the longer length intervals had large fat accumulations in the ovarian membranes, abnormally small eggs and egg numbers ranging from 70 to 500. The 515 normal Florida gar examined averaged 5,209 eggs per female. The fecundity of longnose gar examined by Holloway (1954) ranged from 1,110 to 77,156 eggs

per female for fish 27 to 58 inches long. About 21% of these longnose gar contained over 30,000 eggs.

Netsch and Witt (1962) reported fecundities of 4,273 to 59,422 eggs per female for 26 longnose gar 30.2 to 53.9 inches long. Fifty percent of the females contained 30,000 or more eggs. The average fecundity was 27,830 eggs per female or 3002 eggs per pound of body weight. This figure compares with 2411 to 2526 eggs/per pound for the two largest longnose gar examined by Holloway (1954) and 4051 eggs/per pound for the shortnose gar reported by Potter (1926).

Early development and growth - Carlander (1969) indicated that the bright green eggs of shortnose gar are deposited in small masses held together by a clear gelatinous substance which attaches to weeds. The diameter of shortnose gar eggs has not been reported. Netsch and Witt (1962) reported that both longnose and shortnose gar eggs are toxic to higher vertebrates such as chickens and mice. A mouse force fed 0.2 ml of homogenized shortnose gar eggs died in less than 18 hr. Netsch and Witt (1962) found gar eggs in the digestive tracts of a bluegill and a river carpsucker and thus concluded that they may not be toxic to fishes.

Richardson (1913) and Potter (1926) reported incubation times of 8 to 9 and 8 days, respectively, for shortnose gar eggs. Echelle and Riggs (1972) concluded that most young-of-the-year gars in Lake Texoma hatched between late April and early June in 1965 and that the peak hatching period was early May. Five shortnose gars identified to species hatched between April 13 and May 26 in Lake Texoma. Gowanloch (1933) noted that

"short-nosed" gar eggs sometimes hatch even when receding waters leave them exposed above the surface.

Echelle and Riggs (1972) assumed that shortnose gar are 8 mm in total length at hatching. Riggs and Moore (1960) found that the growth rates of six young spotted gar reared in aquaria ranged from 1.3 to 2.3 mm per day and averaged 1.7 mm per day. Echelle and Riggs (1972) surmised that these growth rates are applicable to shortnose gar since the eggs and adults of both species are of similar size and the adults have similar body forms.

Echelle and Riggs (1972) described the early behavioural development of gar in Lake Texoma. Sac-fry are capable of swimming but remain relatively inactive, hanging vertically for long periods, attached to objects in the water using an adhesive structure at the front of their short snouts. In aquaria they commonly attach themselves to the surface film but in Lake Texoma they were found attached only to submerged objects such as vegetation and debris. Shortly after absorption of the yolk sac, fry cease to hang vertically and are able to rest motionlessly in a horizontal position at any depth in the water. At about this stage they take their first aerial breath and become more active. Richardson (1913) indicated that shortnose gar absorb the yolk-sac 7 days after hatching and begin to feed 16 days after hatching.

Although information is scanty, the growth of young-of-the-year shortnose gar appears to be very rapid. Gowanloch (1933) reported that young "short-nosed" gar taken by Garman (1890) in Illinois were 3.5 inches long on July 7 and averaged about 10 inches long by August. Young-of-the-year shortnose gar

captured on July 22 in Lake Texoma were in length intervals between 125 and 214 mm (4.9 and 8.4 inches) (Echelle and Riggs 1972). Other lengths reported for young-of-the-year shortnose gar are given in Table 25.

Table 26 shows the lengths of shortnose gar in each age group in Lewis and Clark Lake, South Dakota. The length-weight relationship of shortnose gar is displayed in Table 27. Equations describing the length-weight relationship are given in Table 28. Walburg (1964) indicated that shortnose gar in Lewis and Clark Lake ranged from 12.0 to 30.3 inches long. In 1962, the average lengths and weights of female and male shortnose gar in Lewis and Clark Lake were 24.5 inches and 1.8 pounds, and 22.5 inches and 1.4 pounds, respectively (Walburg 1964).

The possibility of sexual dimorphism in the growth rate of shortnose gar apparently has not been examined. Netsch and Witt (1962) and Klaassen and Morgan (1974) found that female longnose gar grew faster than males. Holloway (1954) noted that female Florida gar averaged larger than males in small Florida lakes. The greater average size of female shortnose gar compared to males in Lewis and Clark Lake suggests that females of this species also have a faster growth rate, or greater longevity, or both than males.

Table 29 lists the coefficients of condition (K) reported for shortnose gar. No change in K with sex or size is reported except Shields (1955) noted some increase in K with increase in length (Carlander 1969).

Netsch and Witt (1962) aged longnose gar by the annuli on the largest branchiostegal ray. They reported that female

Table 25. Growth of young-of-the-year shortnose gar (from Carlander 1969)

Location	Date	No.	Total length (mm)	
			Mean	Range
Illinois	2 wks after hatching	1	19	-
Illinois R.	May	-	-	15 - 64
Illinois R.	June	1	44	-
Illinois R.	July	1	89	-
Ft. Randall Reservoir	July	1	69	-
L. Okoboji, Iowa	Aug.	-	-	64 - 127
L. Okoboji, Iowa	Oct.	-	-	102 - 152
Ohio	Oct.	-	-	178 - 254

Table 26. The mean total lengths (mm) of shortnose gar in each age group in Lewis and Clark Lake, South Dakota in 1962 (from Walburg 1964).

Age Group	No.	Average Total Length	
		Inches	mm
I	31	16.4	417
II	31	19.1	486
III	60	21.1	536
IV	93	23.1	587
V	26	23.8	605
VI	16	26.4	671
VII	2	28.9	734

Table 27. Total length (mm) - weight (gm) relationship of shortnose gar (from Carlander 1969).

TL	No.	Mean wt.	Wt. range	Citation[1]
279	1	91	-	S472
305	7	91	82 - 91	S472
318	-	132	-	SD
330	2	109	18 - 136	S472
343	-	141	-	SD
368	-	168	-	SD
381	1	172	-	S472
394	-	204	-	SD
419	-	245	-	SD
445	-	295	-	SD
470	-	345	-	SD
483	1	494	-	S472
483	1	635	-	F74
495	-	395	-	SD
508	1	590	-	F74
521	-	477	-	SD
533	2	771	-	F74
546	-	562	-	SD
559	7	821	762 -	S472
559	1	1089	-	F74
572	-	644	-	SD
574	1	867	-	C30
584	3	844	771 - 880	S472
584	3	998	907 - 1043	F74
597	-	757	-	SD
610	1	1134	-	F74
622	-	871	-	SD
635	2	1239	1225 - 1252	S472
648	-	1030	-	SD
660	2	1347	1306 - 1388	S472
673	-	1170	-	SD
698	-	1366	-	SD
711	1	2041	-	F74
724	-	1651	-	SD
726	1	571	-	C30
737	1	2404	-	F74
749	-	1747	-	SD
775	-	1469	-	SD
800	-	1506	-	SD
826	-	1547	-	SD

[1] C30 = Carlander (1949)
F74 = Freeman and Huish (1953)
S472 = Swingle (1965)
SD = South Dakota data based upon 1477 shortnose gar.

Table 28. Equations describing the length (mm) - weight (gm) relationship of shortnose gar (from Carlander 1969).

Author	Location	No.	Size Range	Equation
Shields 1955	Ft. Randall Reservoir	292	483 - 686 mm	log W = -7.533 + 3.122 log TL
Swingle 1965	Alabama	26	279 - 660 mm	log W = -6.53 + 3.43 log TL

Table 29. Coefficients of condition (K) reported for shortnose gar (from Becker 1964 and Carlander 1969).

Location	No.	Size Range[1]	Coefficient of Condition	
			Average	Range
Winnebago L.	5	405 - 483 mm SL	0.55	0.44 - 0.70
Iowa	2	500 - 632 mm SL	0.66	0.62 - 0.69
Alabama	26	279 - 660 mm TL	0.40	0.30 - 0.48
South Dakota	1559	305 - 813 mm TL	0.34	0.31 - 0.40

[1] SL = standard length

TL = total length

longnose gar have a greater longevity than males. Carlander (1969) noted that a shortnose gar was kept in captivity for 20 years.

Food habits - Potter (1926) indicated that young shortnose gar feed on Entomostraca and mosquito larvae. A sixteen-day-old shortnose gar 0.75 inches long contained 17 large cladocerans *(Scapholeberis mucronata)* (Richardson 1913).

Most studies indicate that adult shortnose gar feed primarily on fishes. Forbes (1888) found that 4 shortnose gar stomachs contained a bass *(Micropterus)*, a gizzard shad, minnows and cladocerans. Evermann and Clark (1920) reported that shortnose gar fed mainly on small fishes in Lake Maxinkuckee, Indiana. Potter (1923) listed 5 crayfish *(Cambarus virilis)*, 2 yellow perch *(Perca flavescens)*, 1 bluegill *(Lepomis pallidus)*, 1 pumpkinseed *(Eupomotis gibbosus)*, 1 minnow *(Notropis)*, and the remains of 1 unidentified fish as the contents of 10 shortnose gar stomachs from Lake Okoboji, Iowa. Forage fishes comprised the bulk of the volume of food of shortnose gar in Foots Pond, Indiana (Lagler *et al.* 1942). Shields (1957c) noted that shortnose gar fed heavily on carp until the latter were over 125 mm long. Echelle and Riggs (1972) found that fishes were the main items in the diet of shortnose gar 225 to 272 mm long in Lake Texoma. All fish that Echelle and Riggs (1972) found in gar stomachs were young-of-the-year, except for shiners and occasional adult *Gambusia affinis*. Mississippi silversides *(Menidia audens)* were the most commonly eaten fish.

Echelle and Riggs (1972) demonstrated a progressive increase in the frequency of fishes in the diet with increased size of gar in Lake Texoma (see Table 30). Cladocerans, mainly *Scapholeberis*, comprised the bulk of the food of spotted or shortnose gar 15 or 34 mm long. Fish occurred in 8% of the 24 stomachs containing food. The diet of spotted or shortnose gar 55 to 114 mm long was also numerically dominated by cladocerans, primarily *Scapholeberis*. However, insects and fish were more common than in the smaller gar. Fish occurred in 81% of the stomachs containing food. Fish occurred in all the stomachs of shortnose gar 225 to 272 mm long which contained food.

Lagler *et al.* (1942) observed an apparent seasonal variation in the food of shortnose gar in Foots Pond (see Table 31). The volume of food consumed by shortnose gar in July and August, 1940, was dominated by fish, mainly young gizzard shad. The stomach contents of specimens collected on June 25 and 26, 1941, consisted entirely of crustaceans and insects, mostly small Entomostraca and water-boatmen. Richardson (1913) observed that adult gar came to the surface to seize emerging gnats and mayflies in May and June in Illinois. Similarly, Hunt (1952) noted apparent seasonal variation in the food habits of Florida spotted gar in the Tamiami Canal, Florida. He noted that food intake decreased and the percentage of invertebrates in gar diets increased markedly in late spring.

Echelle and Riggs (1972) noted that the fish most commonly eaten by gar in Lake Texoma (the Mississippi silverside) is also the most abundant fish in the shallows of the lake.

Table 30. Stomach contents of young spotted and shortnose gars in Lake Texoma (from Echelle and Riggs 1972).

Food items	Size groups (mm) and species: Spotted-shortnose* 15 - 34 N**	F	Spotted-shortnose* 55 - 114 N	F	Shortnose 225 - 272 N	F
Crustacea	298	92	162	15		
Cladocera	288	88	162	15		
Scapholeberis	254	54	157	8		
Ceriodaphnia	15	8				
Simocephalus	4	13	3	4		
Chydorus	4	4				
Bosmina	1	4	2	4		
Copepoda	10	6				
Insecta	9	33	18	35	1	13
Zygoptera (nymph)						
Orthoptera			1	4		
Diptera	9	21	16	27		
Tendipedidae	5	21	13	19		
larvae	4	17	4	12		
pupae			9	8		
adults	1	4				
Ceratopogonidae (larvae)	1	4	1	4		
Hemiptera					1	13
Corixidae (adult)					1	13
Aranea						
Pisces	5	8	28	81	8	100
Notropis						
Gambusia			4	12		
Menidia			15	42	1	13
Lepomis						
Micropterus			1	4	2	25
Aplodinotus					1	13
Total number of stomachs	34		33		11	
Per cent of stomach with food	71		79		73	

*Smaller spotted and shortnose gars were not separated to species.

**N refers to the number of organisms; F refers to percent frequency of occurrence in those gars containing food.

Table 31. Food of shortnose gar in Foots Pond, Indiana (from Lagler *et al.* 1942).

Food item	July and August, 1940*			June 25-26, 1941*			Both Periods Combined		
	N**	V	F	N	V	F	N	V	F
Game and Pan Fishes									
White Crappie							1	0.3	1.4
Bass or Sunfish							1	0.5	1.4
Total	2	1.1	10.5				2	0.8	2.8
Forage Fishes									
Gizzard Shad							20	64.7	14.1
Silvery minnow							1	0.3	1.4
Minnows							4	1.2	1.4
Brook Silverside							1	1.0	1.4
Total	26	86.1	68.4				26	67.2	18.3
Fish Remains	7	1.9	26.3				7	1.5	7.0
Crustaceans	1	0.2	5.3	4296	84.0	75.0	4297	18.6	56.3
Insects	39	10.7	31.6	219	16.0	92.3	258	11.9	76.1

*The stomachs of 19 and 52 specimens collected during July and August, 1940, and on June 25-26, 1941, respectively, were examined.

**N refers to the number of organisms; V refers to the percentage of the total volume of food; F refers to the percentage frequency of occurrence.

They concluded that availability is therefore a major factor affecting the king of food consumed by gars. Holloway (1954) observed that the forms most often occurring in Florida gar stomachs were those most common in the habitats from which the gar were collected.

Gowanloch (1933) and Hunt (1960) described the feeding behaviour of gars. This behaviour consisted of a "slow but continuous stalk, seemingly intended to place the anterior half of the snout parallel with and two to three inches from the intended prey, which would then be seized by a sideways snap of the jaws." Carlander (1969) noted that shortnose gar have been observed to line up along shore in 100 to 250 mm of water, with their tails toward shore, waiting until prey were in easy reach.

Echelle and Riggs (1972) concluded that the scarcity of benthic organisms and abundance of surface organisms in gar stomachs suggest that much of the feeding of gars is surface oriented. They noted that the most abundant entomostracan *(Scapholeberis)* in gar stomachs is a form that "glides along the underside of the surface film" (Ruttner 1964) and that Mississippi silversides, the most common fish in gar stomachs in Lake Texoma, tend to rest near the surface at night. They suggested that the amount of surface feeding by gars is probably affected by their air-breathing habit, which occurs at a high rate at the elevated summer temperatures in the shallow waters of Lake Texoma.

Coker (1930) and Lagler *et al.* (1942) reported that 66% and 46%, respectively, of shortnose gar stomachs examined

were empty. Similar high incidences of empty stomachs are reported for longnose, spotted and Florida gars (Scott 1938, Lagler *et al.* 1942, Hunt 1952, Holloway 1954, Goodyear 1967). Lagler *et al.* (1942) suggested that these high incidences of empty gar stomachs may result from very rapid digestion, regurgitation of food on capture or very marked periodicity in feeding. However, Hunt (1952) found no evidence of regurgitation of food despite close observation of the capture of many Florida spotted gar in gill nets. The possibility of a periodicity in the feeding of shortnose gar has not been examined but evidence of such a periodicity exists for other gar species. Holloway (1954) observed Florida gar feeding during all hours of the day but more frequently on cloudy days and on moonlight nights. Hunt (1960) found that Florida gar feeding in aquaria is apparently inhibited by bright illumination. Most longnose gar feeding along the Mississippi coast apparently occurs between 1200 and 0600 hr (Goodyear 1967). Periodicity in the feeding of spotted gar along the Mississippi coast is apparently related to tides not time of day (Goodyear 1967).

Scott (1938) attributed the high incidence of empty longnose gar stomachs to a rapid rate of digestion. Netsch and Witt (1962) found that longnose gar averaging 291 mm long completely digested three minnows averaging about 2.8 gm in total weight within 24 hours. However, Florida gar show a much slower digestion rate, completely digesting multiple-unit meals of 2.5 gm in 42 to 47 hours, with an average of 42 hours (Hunt 1960). The digestion rate of shortnose gar is

probably more similar to that of Florida gar than that of longnose gar.

Rates of food consumption also appear to vary greatly among different species of gars. Longnose gar averaging about 21 gm in weight consumed an average of 9.1% of their body weight per day (Netsch and Witt 1962). They also showed a low average food conversion factor (2.34), indicating a high metabolic efficiency (Netsch and Witt 1962). Two small Florida gar (30 and 35 gm) had an average daily food consumption of 4.26% of their body weight (Hunt 1960). The average daily food consumption of Florida gar weighing about 100 gm was 2.81% of their body weight (Hunt 1960). Again, the rate of food consumption of shortnose gar is probably more similar to that of Florida gar than that of longnose gar.

Parasites and predators - The parasites of shortnose gar are listed in Table 32. Young gar are not known to be an important food of any fish species (Lagler *et al.* 1942). The rapid growth rates and hard scales of young gars probably remove them from any significant predation early in life.

Gar control - Gars are highly piscivorous, competing for food with predaceous game-fishes and eating fishes of greater value to man than are the gars (Holloway 1954). Accordingly, gar control has been considered as useful method of improving waters for angling (Lagler *et al.* 1942, Holloway 1954). However, an increase in the harvest of desirable species as a result of gar reduction remains to be clearly demonstrated

Table 32. Parasites of the shortnose gar, *Lepisosteus platostomus*, listed by Hoffman (1967).

Order	Species
Trematoda	*Macroderoides spiniferus* *Paramacroderoides echinus*
Cestoda	**Proteocephalus ambloplitis* *P. perplexus* *P. singularis*
Nematoda	**Contracaecum spiculigerum*
Acanthocephala	*Leptorhynchoides thecatus*
Crustacea	*Argulus lepidostei* *A. mississippiensis* *Ergasilus elegans* *Lernaea variabilis*

*Larval forms

(Holloway 1954). Gowanloch (1933) wrote that "their voracity is responsible for the destruction of great numbers of useful and valuable fishes". However, the studies cited above suggest that the voracity of gars, at least of some species such as the Florida gars, is not as great as early workers maintained. For example, the daily voluntary food consumptions of warmouth *(Lepomis gulosus)* and largemouth bass are 1.6 and 2.5 times, respectively, as much as that of Florida gar of a similar weight (Hunt 1960).

Gars attain spectacular densities in some waters. In these situations, even species with irregular feeding habits and low food consumption, such as the Florida gar, probably suppress other fishes. For example, Hunt (1952) noted a phenomenal abundance of Florida spotted gar in the Tamiami Canal, Florida, where as many as 270 gar have been counted in 100 yards of canal. Hunt (1952) concluded that "unquestionably the populations of largemouth bass and pan fish in the Tamiami Canal are adversely affected by the predation and competition of the gar."

Lagler *et al.* (1942) listed the following means of controlling gar populations: spearing, shooting, seining, gill netting, trap netting, eletrofishing, poisoning, dynamiting and angling. They noted that gill netting was very destructive of other fishes and that fyke (hoop) nets were relatively unproductive in Foots Pond. Gowanloch (1939) described "gar-trap - game-fish-escape" type hoop nets which allow selective trapping of gars. Gowanloch (1939) suggested the adjustment of trapping operations to take

advantage of the mass spawning activities attributed to gars. Burr (1931) described the use of electricity for gar control. By proper regulation of current, only gars were reported to be killed.

Summary

The shortnose gar occur in the Mississippi drainage from South Dakota to the Ohio Valley and south to Alabama and Texas and in Lake Winnebago in the Great Lakes drainage. In Ohio, they inhabit lowland lakes, oxbows and backwaters, apparently avoiding strong currents and preferring clear waters. In Kansas, adult shortnose gar occupy the deeper water and stronger currents of the mainstreams of rivers. Adults were captured in water less than 1.5 feet deep between large beds of submergent aquatics in Lake Winnebago. Young gar prefer shallow calm water near emergent vegetation and move further from shore as their size increases. Seasonal variations in distribution have not been examined for shortnose gar but have been described for the similar Florida gar.

Gar are apparently very localized in activity. Young gar spend much time resting motionlessly near shore during daylight but commonly swim actively in shallow open waters at night. Shortnose gar may move in schools both before and after but apparently do not undertake extensive seasonal migrations.

Although gars are generally quite tolerant of brackish and salt water, shortnose gar appear to be confined to freshwater.

Aerial breathing allows gar to tolerate very low dissolved oxygen levels. A thermal preferendum of 65 to 75°F is suggested for spotted gars.

Shortnose gar spawn from May to August. In South Dakota, they spawn between late May and mid-July at water temperatures between 19 and 23.5°C. Spawning apparently occurs in shallow weedy, grassy, or "willow grown" areas. Shortnose gar spawn in about 12 to 35 inches of water in Illinois and usually at water depths of less than one foot in the Fort Randall Reservoir, South Dakota.

All shortnose gar over 508 mm long were mature in Lewis and Clark Lake, South Dakota. A few males and females mature at lengths of 457 and 483 mm, respectively, in South Dakota.

Sex ratios in shortnose gar populations have not been examined. Sex ratios range from 0.36 to 3.07 and 0.43 to 2.27 males per female for longnose and Florida gar, respectively, in Florida. A sharp decline in sex ratio with increasing age indicates a shorter lifespan for male than female longnose gar in Missouri.

A 4082 gm female shortnose gar contained 36,460 eggs. The fecundities of Florida and longnose gars range from 1,125 to 15,450 eggs per female for Florida gar and 1,110 to 77,156 and 4273 to 59,422 eggs per female for longnose gar in Florida and Missouri, respectively.

Shortnose gar lay bright green eggs in small masses held together by a clear gelatinous substance which attaches to weeds. Shortnose gar eggs are smaller than those

of longnose gar, which range from 2.1 to 3.2 mm in diameter when preserved. Gar eggs are toxic to higher vertebrates. Shortnose gar eggs hatch in 8 to 9 days.

Shortnose gar are probably about 8 mm in total length at hatching. Sac-fry remain relatively inactive, attaching to submerged objects using an adhesive structure on their snouts. Fry absorb the yolk-sac and begin to feed about 7 and 16 days after hatching, respectively. Young-of-the-year shortnose gar grow very rapidly, reaching lengths of about 2.5 to 10 inches by August. Coefficients of condition and the age-length and weight-length relationships of shortnose gar are shown in Tables 26, 27, 28 and 29. Sexual dimorphism in growth rates has apparently not been examined for shortnose gar but occurs in longnose and possibly Florida gars. Shortnose gar may live up to 20 year in captivity.

Young shortnose gar feed on Entomostraca, mosquito larvae, and other insects. Their main food is the cladoceran *Scapholeberis*. Fishes and insects become more common in shortnose gar diets as size increases. Adult shortnose gar feed primarily on small fishes. Small entomostracans and insects such as water-boatmen and emerging gnats and mayflies are sometimes major components of the diet of adult shortnose gar in May and June.

The feeding behaviour of gars consists of a slow stalk until they prey can be seized by a sideways snap of the jaws. Availability may be a major factor affecting the kind of food eaten by gars. Gar feeding appears to be largely surface oriented.

High incidences of empty stomachs are reported for shortnose gar. This may result from a rapid rate of digestion or a periodicity in feeding. Spotted, Florida and longnose gars show a periodicity in feeding related to illumination, time of day, or tides. Rates of digestion are rapid for longnose gar but slow for Florida gar.

The parasites of shortnose gar are listed. Gars are probably subject to little predation.

Although gars are highly piscivorous, the usefulness of gar control in improving waters for angling has yet to be clearly demonstrated. In some waters, such as the Tamiami Canal, Florida, gars attain phenomenal densities. In these waters, even species with relatively low food consumption, such as the Florida gar, undoubtably adversely affect populations of other fishes. Methods of gar control may be effected by spearing, shooting, seining, gill netting, trap netting, electrofish, poisoning, dynamiting and angling.

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Table 13. Fish species preying on gizzard shad.

Author	Location	Species Preying on Gizzard Shad
Wickliff and Trautman (1931)	Ohio ponds and lakes	white bass *(Morone chrysops)* largemouth bass *(Micropterus salmoides)* and white crappie *(Pomoxis annularis)*
Lagler, Obrecht and Harry (1943); Lagler and Ricker (1943)	Foots Pond, Indiana	gars *(Lepisosteus platostomus, L. productus, L. osseus)*, white bass, largemouth bass, white crappie and black crappie *(Pomoxis nigromaculatus)*
Bonham (1941)	Texas	*L. productus, L. osseus*
Forbes (1888)	Illinois	skipjack *(Alosa chrysochloris)*, northern pike *(Esox lucius)* yellow bullhead *(Ictalurus natalis)* and white crappie
Forbes (1903)	Illinois River	walleye *(Stizostedion vitreum)*, sauger *(S. canadense)*, and yellow bass *(Morone mississippiensis)*
Dendy (1946b)	Norris Reservoir Tennessee	channel catfish *(Ictalurus punctatus)*, largemouth bass, smallmouth bass *(Micropterus dolomieui)* spotted bass *(M. punctulatus)*, black crappie, walleye, sauger, freshwater drum *(Aplodinotus grunniens)*.
Eschmeyer (1944)	Clinch River Tennessee	white bass, largemouth bass
Summerfelt (1968)	Oklahoma reservoirs	flathead catfish *(Pylodictus olivarus)*, freshwater drum, and longnose gar *(L. osseus)*
Kutkuhn (1958)	North Twin Lake, Iowa	yellow bass, yellow perch, walleye, black crappie, largemouth bass, black bullhead
Jester (1962)	Conchas Lake, New Mexico	largemouth bass, white crappie, black crappie, channel catfish, walleye, black bullhead, yellow bullhead, blue catfish and a single rainbow trout *(Salmo gairdneri)*

Jester and Jensen (1972)	Elephant Butte Lake, New Mexico	northern pike, walleye, channel catfish, white bass, largemouth bass
Lagler and Hubbs (1940)		bowfin *(Amia calva)*
Galligan (1951)	Cayuga Lake, New York	lake trout *(Salvelinus namaycush)* (a single gizzard shad was found in one of 312 stomachs examined)

Table 16. Total length-weight relationship of paddlefish. Lengths are in mm and weights in gm (from Carlander 1969).

TL	No.	Mean Wt.	Range
76-101	3	5	-
152-177	1	7	-
178-202	8	36	14-36
208-228	6	18	14-18
	2	26	-
229-253	14	27	23-36
254-278	25	36	32-45
	5	68	59-86
279-304	19	50	45-59
	7	100	86-127
305-329	11	59	50-73
	7	127	113-141
330-355	5	100	73-136
	2	154	-
356-380	2	200	-
381-405	1	136	-
	1	227	-
406-431	1	177	-
	1	254	-
432-457	3	200	181-213
458-482	2	249	227-272
	2	322	281-363
483-507	2	240	227-254
508-532	10	281	227-363
	1	399	-
533-558	6	426	-
	3	553	481-590
559-583	5	345	272-454
	2	726	680-771
584-609	19	508	454-613
	3	735	481-907
610-634	12	568	454-680
635-659	15	671	318-1089
660-685	15	726	567-907
	4	998	821-1179
686-710	7	857	680-1043
	8	1103	853-1497
711-736	13	1052	680-1406
737-761	8	1125	953-1497
	6	1511	1161-1874
762-786	30	1107	907-1361
	10	1715	1220-2631
	1	1950	-
787-812	4	1243	1021-1451
	7	1669	1361-2096
813-837	4	1451	1225-1905
	15	1887	1420-2767

	12	1950	1565-2676
864-888	3	1987	1588-2223
	16	2291	1729-2722
889-913	6	1850	1474-2041
	22	2318	1814-3606
914-939	31	2571	2041-3343
940-964	31	2849	2354-4264
965-1015	95	3066	1928-5049
1016-1066	57	4042	2948-6350
1069-1117	42	4904	3402-7938
1118-1167	29	5475	4082-7484
1168-1218	20	6858	5216-8800
1219-1269	13	8128	6350-11140
1270-1320	8	9707	8391-11567
1321-1399	5	11998	8165-16216
1372-1410	4	12673	9979-18597
1422-1453	3	16974	14061-18597
1778	1	35834	-
1880	2	62052	56020-68040
2210	1	31751	-
2235	1	56020	-

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